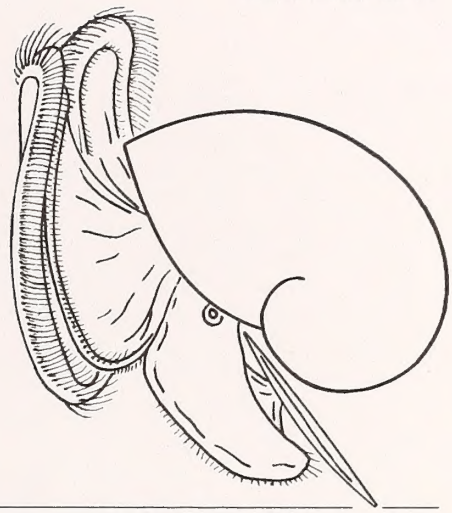
ISSN 0042-3211

THE VELIGER



A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler (1901–2000), Founding Editor

Volume 48 June 30, 2006 Number 1

CONTENTS

The Veliger (ISSN 0042-3211) is published quarterly in January, April, July, and October by the California Malacozoological Society, Inc., % Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Periodicals postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to *The Veliger*, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

THE VELIGER

Scope of the journal

The Veliger is an international, peer-reviewed scientific quarterly published by the California Malacozoological Society, a non-profit educational organization. *The Veliger* is open to original papers pertaining to any problem connected with mollusks. Manuscripts are considered on the understanding that their contents have not appeared, or will not appear, elsewhere in substantially the same or abbreviated form. Holotypes of new species must be deposited in a recognized public museum, with catalogue numbers provided. Even for non-taxonomic papers, placement of voucher specimens in a museum is strongly encouraged and may be required.

Very short papers, generally not over 750 words, will be published in a "Notes, Information & News" column; in this column will also appear notices of meetings and other items of interest to our members and subscribers.

Membership and Subscription

Affiliate membership in the California Malacozoological Society is open to persons (not institutions) interested in any aspect of malacology. New members join the society by subscribing to *The Veliger*. Rates for Volume 48 are US $50.00 for affiliate members in North America (USA, Canada, and Mexico) and US $88.00 for libraries and other institutions. Rates to members outside of North America are US $65.00 and US $98.00 for libraries and other institutions. All rates include postage, by air to addresses outside of North America.

Memberships and subscriptions are by Volume only and follow the calendar year, starting January 1. Payment should be made in advance, in US Dollars, using checks drawn from US banks or by international postal order. No credit cards are accepted. Payment should be made to *The Veliger* or "CMS, Inc." and *not* the Santa Barbara Museum of Natural History. Single copies of an issue are US $25.00, postage included. A limited number of back issues are available.

Send all business correspondence, including subscription orders, membership applications, payments, and changes of address, to: The Veliger, Dr. Henry Chaney, Secretary, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105, USA.

Send manuscripts, proofs, books for review, and correspondence regarding editorial matters to: Geerat Vermeij, Department of Geology, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA.

The Veliger 48(1):1–7 (June 30, 2006)

THE VELIGER

Effects of a Hen's Egg Yolk Diet on Certain Inorganic Elements in the Snail *Helisoma trivolvis* (Colorado Strain)

JOYCE H. L. ONG, MICHAEL CHEJLAVA
Department of Chemistry, Lafayette College, Easton, Pennsylvania 18042, USA
BERNARD FRIED*
Department of Biology, Lafayette College, Easton, Pennsylvania 18042, USA
AND
JOSEPH SHERMA
Department of Chemistry, Lafayette College, Easton, Pennsylvania 18042, USA

Abstract. Graphite furnace atomic absorption spectrometry, flame atomic absorption spectrometry, and ion chromatography were used to investigate several elements in the whole body, digestive gland-gonad complex (DGG), shell, and plasma of the pulmonate snail, *Helisoma trivolvis* (Colorado strain), maintained in artificial spring water (ASW) on two different diets, hen's egg yolk (Y) and Romaine leaf lettuce (L). Whole body and DGG samples were analyzed for the following seven elements: sodium, potassium, calcium, magnesium, zinc, iron, and manganese. Of these, iron was present in a significantly higher concentration (Student's *t*-test, $P < 0.05$) in the whole bodies of snails on the L-diet compared to those on the Y-diet. For the DGG analysis, calcium and potassium were present at significantly higher concentrations, and magnesium at a significantly lower concentration, in snails on the L-diet. Plasma was analyzed for calcium and iron, and no significant differences were found in the concentrations of these elements in snails on both diets. The shells of *H. trivolvis,* analyzed only for calcium, showed no statistical difference in the concentration of this element between snails on the L-diet versus those on the Y-diet. The Romaine leaf lettuce, the hen's egg yolk, and the ASW were analyzed for certain elements: food samples for potassium, magnesium, calcium and iron, and ASW for calcium and iron. There were significantly higher concentrations of calcium and iron in the hen's egg yolk compared to the Romaine leaf lettuce (Student's *t*-test, $P < 0.05$). The ASW contained calcium at a concentration of 20.0 ± 0.0 mg L^{-1}, and a trace amount of iron at 0.0307 ± 0.017 mg L^{-1}. The occurrence of certain elements in the snail may be considered as the ultimate result of passage of these elements from the lettuce or egg yolk upon which the snails were fed or the water in which they were maintained.

INTRODUCTION

Helisoma trivolvis (Say, 1816) is a ubiquitous fresh water planorbid snail in North America. Numerous strains of this snail have been reported, but the taxonomic relationships within the species are still uncertain. One of us (BF) has maintained two strains of *H. trivolvis* in the laboratory for a number of years. One strain, *H. trivolvis* (Pennsylvania strain), is heavily pigmented with melanin and has a black body. This strain serves as a vector of the 37-collar-spined echinostome, *Echinostoma trivolvis* (Cort, 1914), in the USA (see Huffman & Fried, 1990 for a review). The second strain, *H. trivolvis* (Colorado strain), is refractory to infection with *E. trivolvis,* lacks melanin, and has an orange-red body. The Colorado strain has been used extensively in neurobiology studies (see Kater, 1974).

Two of us (BF and JS) used a high fat diet (hen's egg yolk) in the late 1980s to induce hyperlipidemia and hyperlipemia in the medically important planorbid snail *Biomphalaria glabrata* (Say, 1816) (see reviews in Fried & Sherma, 1990, 1993). In addition to studies on neutral and polar lipids in the snails maintained on the high fat diets, recent work examined carbohydrates (Kim et al., 2001) and lipophilic pigments (Kim et al., 2002; Evans et al., 2004) in such snails. Recently, our laboratory has examined the lipid composition of *H. trivolvis* (Co) in snails maintained on a hen's egg yolk diet. As expected, both juvenile and adult snails maintained on this diet accumulated significant amounts of certain lipids compared to cohorts maintained on a lettuce leaf diet (Schneck et al., 2003a, b).

There are no studies on elements in snails raised on

* Author to whom correspondence should be addressed. Telephone: (610)330-5463; fax: (610)330-5705, e-mail: friedb@lafayette.edu.

various diets, and the present study was designed to determine the effects of a high fat diet (hen's egg yolk) on the element composition of *H. trivolvis* (Co) snails. Elements in the snails raised on the high fat diet were compared with those of snails maintained on a low fat diet (Romaine lettuce leaf). Previous studies have examined certain elements in snails independent of diet or infection with larval trematodes. Some of these representative studies and their findings are the following: Layman et al. (1996a) used atomic absorption spectrometry (AAS) and inductively coupled plasma-atomic emission spectrometry (ICP-AES) to study metal ions in the DGGs of *H. trivolvis* (PA) infected with *E. trivolvis* and uninfected *H. trivolvis* snails. They found sodium present in significantly higher amounts, and magnesium and manganese in significantly lower amounts, in the infected versus uninfected DGGs. Layman et al. (1996b) measured metallic ions in *B. glabrata* snails infected with *E. caproni* and in uninfected snails by ICP-AES and found no significant differences (Student's *t*-test, $P > 0.05$) in the concentrations of the metals in whole infected versus whole uninfected snails. Kaufer et al. (2002) analyzed the effects of *Euhaplorchis californiensis* Martin, 1950 infection on the metal ion concentrations in the DGGs of the marine snail *Cerithidea californica* Haldeman, 1840 by graphite furnace atomic absorption spectrometry (GFAAS) and ion chromatography (IC) and reported calcium present in significantly higher amounts, and magnesium in significantly lower amounts, in infected versus uninfected DGGs. Ong et al. (2004) investigated the effects of *Schistosoma mansoni* Sambon, 1907 infection on inorganic elements in the whole bodies of *B. glabrata* snails and reported significantly higher amounts of calcium, cadmium, manganese, and sodium in the whole infected versus whole uninfected snails.

Because there are no previous studies on the effects of a high fat diet on the element content of planorbid snails, the purpose of this study was to examine certain elements in *H. trivolvis* (Co) maintained on a hen's egg yolk diet. Controls consisted of cohort snails maintained on a diet of Romaine leaf lettuce.

MATERIALS AND METHODS

Snail Maintenance

Stock cultures of *H. trivolvis* (Co) were maintained from eggs to sexually mature adults at 23 ± 1°C in aerated glass jars, each containing 10 to 20 snails in 800 mL of artificial spring water (ASW) (Schneck et al., 2003a). The ASW was prepared as described by Ulmer (1970). One culture of 25 snails with shell lengths ranging from 16–20 mm was maintained *ad libitum* on boiled Romaine lettuce leaf (L-diet) for 20 weeks. Another culture of 25 snails (16–20 mm shell length) was first maintained on the L-diet for 16 weeks and then on the boiled hen's egg yolk diet (Y-diet) for an additional four weeks. For all the cultures, food and water were changed twice a week.

Sample Preparation

All glassware used for sample preparation and element analysis was cleaned as follows: first washed with soap and rinsed with tap water, soaked in 10% nitric acid solution for at least 2 hr, rinsed with deionized water at least three times, and finally dried in an oven overnight at 250°C. These steps were performed to ensure removal of any elements adhering to glass surfaces. Trace metal grade nitric acid (Fisher Scientific, Fair Lawn, New Jersey) was used in all experiments throughout this research.

Whole Body, Digestive Gland-Gonad Complex (DGG), and Shell

The whole bodies, DGGs, and shells of 10 individual snails (n = 10) on each diet (lettuce or yolk) were prepared as described below. During sample preparation, all snail dissections were performed in 6 cm diameter petri dishes. The shells of the snails were gently cracked with a blunt forceps, and the snail bodies removed from the shells and weighed (range 50 to 250 mg blotted wet weight). Shell samples were collected at the same time whole body samples were prepared and were obtained as follows: the shell pieces remaining in the petri dish after removal of the snail bodies as described above were collected with a forceps and weighed (range 30 to 120 mg blotted wet weight). For DGG samples, snail bodies were first obtained as described above. Each DGG was then dissected free of the visceral mass under a dissecting microscope with forceps and weighed (range 51 to 100 mg blotted wet weight). The visceral masses were discarded. All samples were rinsed several times with deionized water, and kept moist in 6 cm diameter petri dishes lined with filter paper that had been previously dampened with deionized water. Prior to analysis, each sample (whole body, DGG, or shell) was digested in 2 mL of boiling concentrated nitric acid in a 10 mL beaker. Each digested sample was diluted to 10.00 mL in a volumetric flask with 2% (v/v) nitric acid.

Whole body and DGG samples were analyzed for the following elements: calcium, iron, potassium, magnesium, sodium, manganese, and zinc. Calcium, potassium, magnesium, and sodium were determined by FAAS, and iron, manganese, and zinc by GFAAS. Shell samples were analyzed for calcium by FAAS. To ensure that sample concentrations were within the range of the calibration curve of the standards, the shell samples were diluted 2000-fold with 2% (v/v) nitric acid. For all calcium analyses, a lanthanum (III) nitrate solution [31 g lanthanum (III) nitrate hexahydrate salt diluted in 100 mL 2% (v/v) nitric acid] was added in an amount that was equivalent to 10% of the flask size to remove interfering phosphate ions that prevent the volatilization of calcium. For sodium

analysis, potassium chloride [4 g potassium chloride diluted in 100 mL 2% (v/v) nitric acid] was added in a volume that was 10% of the flask size to suppress ionization of sodium atoms.

Plasma

An additional 20 snails were used to prepare the plasma samples (10 snails each on the L- and Y-diets). Samples of plasma, which is defined as hemolymph minus the hemocyte fraction, were obtained as follows: to obtain hemolymph, snail shells were cracked open gently with a blunt forceps and the hemolymph allowed to ooze out into a dry petri dish. The hemolymph was removed from the petri dish using a Pasteur pipet and pooled in Eppendorf tubes. Hemolymph from three or four snails on the lettuce diet was pooled to prepare a sample of approximately 300 μL. Likewise, hemolymph was pooled from three or four snails on the yolk diet to prepare an approximate 250 μL sample from that population. For each diet, three pools of the hemolymph (n = 3) were prepared from 10 snails.

The hemolymph samples were centrifuged at 5600 × g for 5 min to obtain a pellet (consisting of hemocytes and some residual snail debris) that was discarded, and the supernatant (plasma) was used. The plasma was transferred to a new Eppendorf tube using a Pasteur pipet. The sample was then diluted 10-fold in 0.01 M nitric acid and analyzed for calcium by IC and for iron by GFAAS.

Snail Food

Romaine lettuce and hen's eggs (domestic chickens) were boiled for approximately 10 min prior to use. Only the green, leafy portion of the lettuce and the yolk of the egg were used for analyses. Both foods were blotted dry prior to weighing. Approximately 5 g of lettuce and 1 g of yolk were weighed accurately in separate beakers, and three samples were prepared for each diet (n = 3). The lettuce sample was digested in 37 mL of boiling concentrated nitric acid in a 25 mL beaker until a thin yellow film remained at the bottom of the beaker. The yolk was digested in 32 mL of boiling concentrated nitric acid in a 25 mL beaker. Concentrated sulfuric acid (5 mL) was added to the digest to aid in raising the temperature of the solution. A dark colored film remained at the end of the yolk digestion. For both diets, the resulting film was dissolved in 10 mL in a volumetric flask with 2% (v/v) nitric acid. The lettuce and yolk were analyzed for calcium, iron, potassium, and magnesium by FAAS, and for iron by GFAAS.

Artificial Spring Water (ASW)

Three samples of ASW (n = 3) were collected and analyzed for calcium and iron by FAAS and GFAAS, respectively. The ASW samples were diluted 100-fold for calcium determination and 2-fold for iron determination using 2% (v/v) nitric acid.

Elemental Analysis by Atomic Absorption Spectrometry (AAS) and Ion Chromatography (IC)

GFAAS was utilized to quantify the levels of iron, manganese, and zinc, while FAAS was used to analyze for calcium, potassium, magnesium, and sodium. Calcium determination in the plasma samples was performed by IC because sample volumes were too small to allow the use of FAAS.

The GFAAS instrument was a GBC 932 plus (GBC Scientific Equipment, Arlington Heights, Illinois) atomic absorption spectrometer with GBC GF3000 graphite furnace system, separate hollow cathode lamps (Varian, Inc., Walnut Creek, California) for each element determined, GBC PAL3000 autosampler, and GBC Advanta version 1.33 software. The instrument had a double beam design and a deuterium background correction system. All standard and sample volumes were 20 μL. Stock standard solutions of each metallic ion in 2% HNO_3 were made and autodiluted with 2% HNO_3 into multiple working standards by the instrument. The lamp current and wavelength, slit width, and oven temperature program were optimized for each element. All samples were analyzed in triplicate to obtain mean absorbance values. The instrument provided the experimental concentration of each test solution by interpolation from the calibration curve (mean absorbance versus the working range of the element: 100–2000 μg L^{-1} for Fe and Zn, 25–300 μg L^{-1} for Mn).

The FAAS instrument was a Varian SpectrAA-20 atomic absorption spectrometer (Varian, Inc.) with a 1-lamp turret arrangement, separate hollow cathode lamps (Varian Techtron) for each element determined, and an air-acetylene burner. The instrument had a double-beam design and no background-correction system. Wavelength settings, slit selection, lamp current, and gas flows were optimized for each element. Five standard solutions were prepared for analysis of each element with the following working ranges (mg L^{-1}): Ca 0.20–5.0, Mg 1.0–50, Na 0.040–2.0, K 1.0–50. The standards and samples were analyzed using three 30 s integrations. The instrument provided the experimental concentration of each test solution by interpolation from the calibration curve (mean absorbance versus element concentration).

The IC instrument was a DX-120 ion chromatograph (Dionex, Sunnyvale, California) with an AS40 automated sampler, IonPac CG12A guard column (4 × 50 mm), IonPac CS12A cation exchange analytical column functionalized with weak phosphonic and carboxylic acid groups (4 × 250 mm), and self-regenerating membrane cation suppressor system. The isocratic mobile phase was 20 mM methanesulfonic acid at a flow rate of 0.98 mL/

Table 1

Mean concentration ± standard deviation in mg g^{-1} of wet tissue of whole bodies obtained by FAAS and GFAAS for elements in *H. trivolvis* maintained on the L- and Y-diets.

Element	L-diet[a]	Y-diet[a]	Value of *P*
Ca	5.43 ± 2.8	4.26 ± 1.8	0.292
Fe	0.0187 ± 0.0060	0.0112 ± 0.0036	0.00409[b]
K	1.34 ± 0.34	1.27 ± 0.20	0.628
Mg	0.863 ± 0.25	0.863 ± 0.22	0.998
Mn	0.00632 ± 0.0018	0.00470 ± 0.0032	0.195
Na	0.273 ± 0.054	0.324 ± 0.15	0.331
Zn	0.0647 ± 0.061	0.0446 ± 0.024	0.348

[a] n = 10 samples, where each sample consisted of the whole body of an individual snail.

[b] Differences significant at $P < 0.05$ as determined by the Student's *t*-test.

Table 2

Mean concentration ± standard deviation in mg g^{-1} of wet tissue of the DGGs obtained by FAAS and GFAAS for elements in *H. trivolvis* snails maintained on the L- and Y-diets.

Element	L-diet[a]	Y-diet[a]	Value of *P*
Ca	2.44 ± 0.57	1.68 ± 0.41	0.00329[b]
Fe	0.0406 ± 0.019	0.0234 ± 0.019	0.0602
K	0.927 ± 0.32	0.669 ± 0.18	0.0414[b]
Mg	0.498 ± 0.096	0.648 ± 0.14	0.0119[b]
Mn	0.00185 ± 0.00059	0.00178 ± 0.00056	0.792
Na	0.425 ± 0.14	0.343 ± 0.078	0.122
Zn	0.0254 ± 0.015	0.0431 ± 0.029	0.0829

[a] n = 10 samples, where each sample consisted of the DGG of an individual snail.

[b] Differences significant at $P < 0.05$ as determined by the Student's *t*-test.

min. Three standard calcium solutions with concentrations of 5, 50, and 100 mg L^{-1} were prepared in 0.01 M nitric acid for generation of a linear least-squares calibration curve. The calibration curves and interpolated sample concentrations were obtained using PeakNet Chromatography Workstation software. The injection volumes of standards and samples were 25 µL, and all solutions were analyzed in triplicate.

Data Analysis

For all the three analytical methods (GFAAS, FAAS, and IC), the measured element concentration in the test sample solutions was provided by the instrument by interpolation of bracketed samples from the calibration curve. For the whole body, DGG, shell, and diet samples, the concentration of each element (mg g^{-1}) in the samples was calculated using the following equation:

$$\text{concentration of element} = \frac{(C)(V)(D)}{(M)(1000)} \qquad (1)$$

where C is the test solution concentration from the instrument (mg L^{-1}), V is the volume of the initial dilution of the sample following digestion (10 mL), D is the appropriate dilution factor made for each analysis, and M is the mass of the wet sample (g). The mean concentrations of the elements in the samples obtained from the lettuce fed snails versus the yolk fed snails were statistically compared with the Student's *t*-test (two-sample assuming unequal variances) in Microsoft Excel 2000.

For the plasma and ASW samples, the concentration of the elements (mg L^{-1}) determined were calculated with the following equation:

$$\text{Concentration of element} = (C)(D) \qquad (2)$$

where C is the test solution concentration provided by the instrument (mg L^{-1}), and D is the dilution factor (plasma 10; ASW iron 2, calcium 100). Again, Microsoft Excel 2000 was used to compare for statistical differences in the mean concentrations of the elements in the plasma samples of the snails on the two different diets using the Student's *t*-test ($P < 0.05$).

RESULTS

The seven elements determined in the whole bodies of snails maintained on both diets were present in the following concentration order: calcium > potassium > magnesium > sodium > zinc > iron > manganese. The concentrations of these elements were elevated in snails on the L-diet, with the exception of magnesium, which was present in equal concentrations for snails on both diets, and sodium, which was at a higher concentration in snails on the Y-diet. Iron was the only element with a significantly higher concentration in the whole bodies of snails on the L-diet compared to the snails on the Y-diet (Student's *t*-test, $P < 0.05$). Table 1 lists quantitative data for the snail mass-adjusted concentrations of the elements, calculated using Equation 1, for the whole bodies of *H. trivolvis* (Co) on both diets. The same seven elements were quantified in the DGGs. Table 2 lists quantitative data for the snail mass-adjusted (calculated using Equation 1) element concentrations in the DGGs of *H. trivolvis* (Co) snails on both the L- and Y-diets. For DGGs of snails on the Y-diet, the elements were present in a concentration order similar to the one in the whole bodies of the snails described above. The DGGs of the snails maintained on the L-diet showed the following order in concentration of the elements: calcium > potassium > magnesium > sodium > iron > zinc > manganese. These elements were all present at higher concentrations in DGGs of snails on the lettuce diet with the exception of magnesium and zinc, which were at lower concentrations compared to DGGs of snails on the Y-diet. There was a

Table 3

Mean concentration ± standard deviation in mg g^{-1} obtained by FAAS and GFAAS for the wet weights of Romaine leaf lettuce and hen's egg yolk.

Element	Lettuce[a]	Egg yolk[a]	Value of *P*
Ca	0.989 ± 0.23	1.85 ± 0.27	0.0138[b]
Fe	0.00468 ± 0.0012	0.0148 ± 0.0026	0.00839[b]
K	1.78 ± 0.64	1.27 ± 0.063	0.303
Mg	0.252 ± 0.073	0.287 ± 0.024	0.509

[a] n = 3 samples, where the lettuce samples were approximately 5 g each, and the egg yolk samples were approximately 1 g each.
[b] Differences significant at $P < 0.05$ as determined by the Student's *t*-test.

significantly lower concentration of calcium and potassium, and a significantly higher concentration of magnesium, in the DGGs of snails maintained on the egg yolk diet than those maintained on the lettuce diet (Student's *t*-test, $P < 0.05$).

The concentrations of calcium (calculated using Equation 1) in the shells of *H. trivolvis* (Co) on the L- and Y-diets were 389 ± 54 mg g^{-1} and 378 ± 62 mg g^{-1}, respectively, and were not significantly different (Student's *t*-test, $P > 0.05$). The plasma samples, analyzed only for calcium and iron, gave the following results (calculated using Equation 2): 278 ± 43 mg L^{-1} and 233 ± 9.7 mg L^{-1} in snails on the L- and Y-diet, respectively, for the calcium analysis; 10.3 ± 1.2 mg L^{-1} and 10.1 ± 1.6 mg L^{-1} in snails on the L- and Y-diet, respectively, for the iron analysis. No significant differences were found between the concentrations of both elements in the plasma of snails maintained on both the L- and Y-diet (Student's *t*-test, $P > 0.05$).

The results obtained for certain elements in Romaine lettuce leaf and hen's egg yolk are summarized in Table 3. These foods were analyzed for the elements calcium, iron, potassium, and magnesium. Among these four elements determined, the calcium and iron concentrations in the hen's egg yolk were significantly higher than those found in the lettuce (Student's *t*-test, $P < 0.05$).

The results for the calcium and iron determination in the ASW (calculated using Equation 2) were 20.0 ± 0.0 mg L^{-1} and 0.0307 ± 0.017 mg L^{-1} for calcium and iron, respectively. According to the standard water hardness classification of the United States Geological Survey, this calcium concentration indicates that the ASW is of a slightly hard level.

DISCUSSION

The elements that were analyzed in this investigation were selected for several reasons. First, potassium, magnesium, sodium, and calcium are among the elements known to be of highest concentrations in many biological systems (Prosser, 1973). These elements have diverse functions in animal cells and are necessary for normal cellular functions. For instance, calcium, potassium, and magnesium are important for muscle contraction and nerve cell function. The construction of skeletal and shell components is dependent on calcium and magnesium. Magnesium is also an essential cofactor for some enzymes, including the ATPases and kinases (Prosser, 1973). Iron, present in the heme portion of the oxygen carrier hemoglobin, was selected based on visual observations during laboratory work that the colors of the hemolymph of the snails maintained on the lettuce versus yolk diets were different. Snails fed the lettuce diet had hemolymph that was bright red while snails fed the yolk diet had hemolymph that was yellow-orange. The heavy metals zinc and manganese are necessary in trace amounts in biological systems, but are toxic in high concentrations (Prosser, 1973). Zinc and manganese both act as cofactors of certain enzymes found in living systems.

The results obtained are similar to those of Kalyani (2001), who examined certain elements in the giant African land snail, *Achatina fulica* Bowdich, 1822, and estimated calcium to be the major element in both the soft body and shell, followed by potassium, magnesium, and sodium. We found the same order in the concentrations of these elements in the whole bodies and DGGs of *H. trivolvis* (Co) on the L- and Y-diets.

The whole body analysis of *H. trivolvis* (Co) included the major regions of the snail, i.e., the head-foot, viscera, and DGG. The significant depletion of iron in the snail whole bodies on the Y-diet, compared to snails on the L-diet, possibly reflects the presence of blood sinuses in the viscera and head-foot regions of yolk-fed snails, which contain low iron content in the hemolymph and tissue.

The snail DGG (particularly the digestive gland portion) is the main site of interest in dietary studies because it is a good indicator of snail metabolic activity. The DGG contains the digestive gland or hepato-pancreas (liver) and the reproductive glands of the snail, the ovotestis. A major function of DGG cells is the storage of various metals held in membrane-insoluble granules in the cells (Howard et al., 1981; Simkiss, 1981; Dallinger & Wieser, 1984; Bebianno & Langston, 1995). Furthermore, the DGG is an important target site for most metabolic and enzymatic activities (Dallinger & Wieser, 1984; Bebianno & Langston, 1995). In our study, calcium and potassium were significantly higher, and magnesium significantly lower, in the DGGs of snails on the L-diet compared to the Y-diet. The DGGs of the yolk-fed snails were yellow-white, in contrast to the DGGs of the lettuce-fed snails, which were dark green-brown. Schneck et al. (2003a) and Evans et al. (2004) made similar observations on the gross appearance of DGGs from snails on the two diets. This color difference may reflect an increased deposition of fat in the DGGs of the yolk-fed

snails, and a subsequent alteration in the element concentrations.

Red blood, due to hemoglobin dissolved in the plasma, is characteristic of planorbid snails. We analyzed iron in the plasma to see if there were differences in the concentration of this element in the snails on the two diets. Schneck et al. (2003a) reported that snails on the L-diet yielded more hemolymph compared to the Y-diet (100 μL and 50 μL per snail, respectively). Furthermore, snails fed the L-diet had a red hemolymph compared to the yellow-orange color in snails on the Y-diet. These observations suggested that the hemoglobin content, and perhaps the iron content, was different in both snail populations. However, the iron concentration was not significantly lower in the yolk-fed snails as compared to the lettuce-fed snails (Student's *t*-test, $P > 0.05$). The color difference in the plasma of the snails probably reflects the presence of lipophilic pigments, i.e., carotenes and xanthophylls, in the plasma of snails maintained on the yolk diet.

The shells of *H. trivolvis* (Co) were analyzed only for calcium, the chief constituent of shells. The calcium concentrations in the shells of snails fed the L- and Y-diets were determined to be 389 ± 54 mg g^{-1} and 378 ± 62 mg g^{-1}, respectively. According to Marxen et al. (2003), the constituents of the molluscan shell are calcium carbonate, present in a concentration of 95 to 99.9%, and organic material, 0.1 to 5%. Calcium carbonate is the insoluble product of the two major inorganic ions in pulmonate shells, calcium and bicarbonate; both ions are obtained from the animal's nutrients and the environment, with bicarbonate being additionally drawn from the animal's metabolic production of carbon dioxide (Luchtel et al., 1997). Calcium carbonate is usually present in one of two predominate crystalline lattice configurations in the pulmonate shell, aragonite or calcite, and sometimes vaterite (Luchtel et al., 1997). Assuming that all of the calcium present in the shell is in the form of calcium carbonate, the percentage of calcium carbonate in the *H. trivolvis* shell obtained in this study is equivalent to 94% and 97% in the lettuce- and yolk-fed snails, respectively.

Schneck et al. (2003a) observed that the shells of *H. trivolvis* (Co) snails maintained on the Y-diet were more fragile and, therefore, more susceptible to cracking than those on the L-diet, suggesting that snails on the Y-diet were lacking calcium in their shells. We found no significant difference in calcium concentration in shells from snails on both diets; hence, shell fragility must be due to factors other than the calcium content of the shell.

Romanoff & Romanoff (1949) reported that the most abundant element in egg yolk is phosphorus, accounting for 0.588% of the yolk's mass. Other inorganic elementals found in egg yolk in small quantities, and their percentages, included calcium (0.144%), magnesium (0.128%), chlorine (0.123%), potassium (0.112%), and sodium (0.070%). Iron and sulfur were present in trace amounts of 0.011% and 0.016% in yolk, respectively. We found that the order of the elements in our egg yolk samples was calcium > potassium > magnesium > iron. The magnesium level in hen's egg yolk in our study was lower than that reported by Romanoff & Romanoff (1949), and this may be attributed to a difference in the method of analysis (method not reported by Romanoff & Romanoff, 1949). Additionally, Romanoff & Romanoff (1949) stressed the important fact that the concentrations of elements in egg yolk, albumen, and shells are dependent upon the concentrations of elements in the diets fed to the hens.

We found no literature on inorganic elements present in Romaine lettuce. Our findings on the elements in Romaine lettuce appear to be the first ever reported. The ASW of Ulmer (1970) is widely used by malacologists and parasitologists to maintain planorbid snails. Our quantitative results on calcium and iron concentrations in this water may be of interest to these workers. The occurrence of certain elements in the snail tissue, plasma and shell may be considered as the ultimate result of passage of these elements from the lettuce or hen's egg yolk upon which the snails were fed, or the water in which they were maintained.

LITERATURE CITED

Bebianno, M. & W. J. Langston. 1995. Induction of metallothionein synthesis in the gill and kidney of *Littorina littorea* exposed to cadmium. Journal of the Marine Biological Association of the United Kingdom 75:173–186.

Dallinger, R. & W. Wieser. 1984. Patterns of accumulation, distribution and liberation of Zn, Cu, Cd, and Pb in different organs of the land snail *Helix pomatia L.* Comparative Biochemistry and Physiology B 79:117–124.

Evans, R. T., B. Fried & J. Sherma. 2004. Effects of diet and larval trematode parasitism on lutein and β-carotene concentrations in planorbid snails as determined by quantitative high performance reversed phase thin layer chromatography. Comparative Biochemistry and Physiology B 137:179–186.

Fried, B. & J. Sherma. 1990. Thin layer chromatography of lipids found in snails. Journal of Planar Chromatography-Modern TLC 3:290–299.

Fried, B. & J. Sherma. 1993. Effects of a high fat diet on the lipid composition of *Biomphalaria glabrata* (Planorbidae: Gastropoda). Trends in Comparative Biochemistry and Physiology 1:941–958.

Howard, B., P. C. H. Mitchell, A. Ritchie, K. Simkiss & M. Taylor. 1981. The composition of intracellular granules from the metal-accumulating cells of the common garden snail (*Helix aspersa*). Biochemistry Journal 194:507–511.

Huffman, J. E. & B. Fried. 1990. *Echinostoma* and echinostomiasis. Advances in Parasitology 29:215–269.

Kalyani, R. 2001. Nutritional studies on soft body and shell of *Achatina fulica* (Pulmonata: Stylommatophora). American Malacological Bulletin 16:195–200.

Kater, S. B. 1974. Feeding in *Helisoma trivolvis*: the morphological and physiological bases of a fixed action pattern. American Zoologist 14: 1017–1036.

Kaufer, S. W., M. Chejlava, B. Fried & J. Sherma. 2002. Effects of *Euhaplorchis californiensis* (Trematoda) infection

on metallic ions in the host snail *Cerithidea californica* (Gastropoda). Parasitology Research 88:1080–1082.

KIM, Y., B. FRIED & J. SHERMA. 2001. Thin layer chromatographic analysis of carbohydrates in *Biomphalaria glabrata* snails maintained on a high fat diet. Journal of Planar Chromatography-Modern TLC 14:61–63.

KIM, Y., B. FRIED & J. SHERMA. 2002. Thin layer chromatographic analysis of lutein and β-carotene in *Biomphalaria glabrata* maintained on a high fat diet. The Veliger 45:256–258.

LAYMAN, L. R., A. C. DORY, K. M. KOEHNLEIN, B. FRIED & J. SHERMA. 1996a. Effects of *Echinostoma trivolvis* (Trematoda) infection on metallic ions in the host snail *Helisoma trivolvis* (Gastropoda). Parasitology Research 82:19–21.

LAYMAN, L. R., A. C. DORY, K. M. KOEHNLEIN, B. FRIED & J. SHERMA. 1996b. Measurement of metallic ions in *Biomphalaria glabrata* (Gastropoda) infected with *Echinostoma caproni* (Trematoda) and in uninfected snails. Journal of the Helminthological Society Washington 63:256–258.

LUCHTEL, D. L., A. W. MARTIN, D.-O. I. INGRITH & H. H. BOER. 1997. Mollusca II. In F. W. Harrison & A. J. Kohn (eds.), Microscopic Anatomy of Invertebrates. Vol. 6B, Mollusca II. John Wiley & Sons, Inc.: New York, NY. 481 pp.

MARXEN, J. C., W. BECKER, D. FINKE, B. HASSE & M. EPPLE. 2003. Early mineralization in *Biomphalaria glabrata*: microscopic and structural results. Journal of Molluscan Studies 69:113–121.

ONG, J. H. L., M. CHEJLAVA, B. FRIED, K. M. KOEHNLEIN, G. L. BOSAVAGE & J. SHERMA. 2004. Effects of *Schistosoma mansoni* infection on inorganic elements in the snail *Biomphalaria glabrata.* Journal of Helminthology 78:343–346.

PROSSER, C. L. 1973. Inorganic ions. Pp. 79–81, 100–102 in C. L. Prosser (ed.), Comparative Animal Physiology. 3rd ed. W. B. Saunders Co.: Philadelphia, PA.

ROMANOFF, A. L. & A. J. ROMANOFF. 1949. Chemical composition. Pp. 355, 359 in The Avian Egg. John Wiley & Sons, Inc.: New York, NY.

SCHNECK, J. L., B. FRIED & J. SHERMA. 2003a. Thin layer chromatographic analysis of neutral lipids and phospholipids in *Helisoma trivolvis* (Colorado Strain) maintained on a high fat diet. The Veliger 46:325–328.

SCHNECK, J. L., B. FRIED & J. SHERMA. 2003b. High-performance thin layer chromatographic analysis of lipids in juvenile *Helisoma trivolvis* (Colorado Strain) maintained on a hen's egg yolk diet. Journal of Planar Chromatography-Modern TLC 16:405–407.

SIMKISS, K. 1981. Cellular discrimination processes in metal accumulating cells. Journal of Experimental Biology 94:317–327.

ULMER, M. J. 1970. Notes on rearing snails in the laboratory. Pp. 143–144 in A. J. MacInnis & M. Voge (eds.), Experiments and Techniques in Parasitology. W. H. Freeman: San Francisco, CA.

The Veliger 48(1):8–16 (June 30, 2006)

THE VELIGER

Habitat Usage by the Page Springsnail, *Pyrgulopsis morrisoni* (Gastropoda: Hydrobiidae), from Central Arizona

MICHAEL A. MARTINEZ*

U.S. Fish and Wildlife Service, 2321 W. Royal Palm Rd., Suite 103, Phoenix, Arizona 85021, USA
(*Correspondent: mike_martinez@fws.gov)

AND

DARRIN M. THOME

U.S. Fish and Wildlife Service, 2800 Cottage Way, Rm. W-2605, Sacramento, California 95825, USA

Abstract. We measured habitat variables and the occurrence and density of the Page springsnail, *Pyrgulopsis morrisoni* (Hershler & Landye, 1988), in the Oak Creek Springs Complex of central Arizona during the spring and summer of 2001. Occurrence and high density of *P. morrisoni* were associated with gravel and pebble substrates, and absence and low density with silt and sand. Occurrence and high density were also associated with lower levels of dissolved oxygen and low conductivity. Occurrence was further associated with shallower water depths. Water velocity may play an important role in maintaining springsnail habitat by influencing substrate composition and other physico-chemical variables. Our study constitutes the first empirical effort to define *P. morrisoni* habitat and should be useful in assessing the relative suitability of spring environments for the species. The best approach to manage springsnail habitat is to maintain springs in their natural state.

INTRODUCTION

The role that physico-chemical habitat variables play in determining the occurrence and density of aquatic microinvertebrates in spring ecosystems has been poorly studied. This field deserves more attention because microfauna play critical roles in energy flow and nutrient cycling in the spring environment, and the sustainability of ecosystems depends upon their persistence (New, 1998). Locally endemic invertebrates such as springsnails (Hydrobiidae), riffle beetles (Elmidae), and amphipods (Amphipoda) can be excellent environmental indicators of aquatic conditions because their presence or absence is often associated with particular chemical and physical conditions (Greeson, 1982; Hershler, 1998).

Numerous invertebrate species are imperiled, particularly those inhabiting aquatic environments. As of November 1, 2004, there were 32 species of snails (aquatic and terrestrial), 70 species of clams, and 21 species of crustaceans listed as threatened or endangered under the Endangered Species Act within the United States (U.S. Fish and Wildlife Service, 2004a). Despite the recognized status of such species, the availability of empirical information on the ecology and biology of these organisms to assist resource managers in developing and implementing effective conservation and recovery programs is limited.

The Page springsnail, *Pyrgulopsis morrisoni* (Hershler & Landye, 1988), is medium-sized relative to other congeners, 1.8 to 2.9 mm in shell height, endemic to the Upper Verde River drainage of central Arizona (Williams et al., 1985; Hershler & Landye, 1988; Hershler, 1994), with all known populations existing within a complex of springs located along Oak Creek near the town of Page Springs, Yavapai County. The species is a candidate for listing as threatened or endangered under the Endangered Species Act (U.S. Fish and Wildlife Service, 2004b). What little is known about the ecology and biology of this species has been obtained through agency status reviews, anecdotal observations, and inferences drawn from literature on other springsnail congeners.

Hydrobiids are strictly aquatic, relying on an internal gill for respiration. Their primary food source is periphyton, and they generally graze on exposed surfaces (Taylor, 1987; Mladenka & Minshall, 2001). *Pyrgulopsis* snails are known to be oviparous. Raisanen (1991) surmised that *P. morrisoni* lay eggs during an annual period of reproduction in the winter. Mladenka & Minshall (2001) found that the Bruneau hot springsnail, *P. bruneauensis* (Hershler, 1990), exhibited recruitment yearround. Among most prosobranchs, the veliger stage is completed in the egg capsule, and upon hatching, individuals emerge into their adult habitat (Brusca and Brusca, 1990). No information is available on death and birth

rates. Significant migration is undocumented although other small aquatic snails have been known to disperse by becoming attached to the feathers or the mud on the feet and legs of waterfowl and shorebirds (Dundee et al., 1967). Predators may include waterfowl, shorebirds, amphibians, fishes, crayfish, leeches, and aquatic insects. No specific information on disease or parasites is available, but other aquatic snails have been known to serve as the intermediate hosts for trematodes.

Springsnails occur in springs, seeps, marshes, spring pools, outflows, and diverse lotic waters, though the most common habitat for *Pyrgulopsis* is a rheocrene, or a spring emerging from the ground as a free-flowing stream (Hershler and Landye, 1988; Hershler, 1998). Springsnails seem to prefer firm substrates such as cobble, rocks, woody debris, and aquatic vegetation, and are rarely found on or in soft sediment (Hershler, 1998; Raisanen, 1991; O'Brien and Blinn, 1999). Distribution of *Pyrgulopsis* within springs has been hypothesized as a function of stable temperature, water chemistry, and flow regime characteristic of the particular aquatic environment within which they occur (Hershler, 1984 and 1998). For example, O'Brien and Blinn (1999) found that dissolved free carbon dioxide plays a significant role in the distribution of the Montezuma Well springsnail, *P. montezumensis* (Hersler and Landye, 1988), and Mladenka and Minshall (2001) found water temperatures influence density and growth rate of *P. bruneauensis.*

Although the current literature provides general insight into ecological conditions suitable for hydrobiids, species-specific information is needed due to the potential for significant inter-specific variation in physiological requirements. Accordingly, the objective of our study was to evaluate associations between habitat variables and occurrence and density of *P. morrisoni* to provide a basic understanding of the species' habitat usage.

STUDY AREA

The Oak Creek Springs Complex includes a number of spring heads located along Oak Creek (Landye, 1973, 1981; Williams et al., 1985; Arizona Game and Fish Department, 1988; Hershler and Landye, 1988). We gained access to Page/Cave Spring, Bubbling Spring, Bass Spring, and an unnamed spring (Figure 1). These aquatic environments are essentially isolated, mid-elevational, permanently saturated, spring-fed aquatic communities commonly described as ciénegas (Hendrickson and Minckley, 1985).

Elevation in the Page Springs area is approximately 1070 meters. Riparian vegetation associated with Oak Creek and the springs complex includes velvet ash, *Fraxinus velutina*; Fremont cottonwood, *Populus fremontii*; Arizona sycamore, *Plantanus wrightii*; willows, *Salix* sp.; and mesquite, *Prosopsis* sp. Aquatic vegetation associated with fine grained sediments, includes macrophytes such as watercress, *Nasturtium officinale*; duckweed, *Lemna minor*; water parsnip, *Berula erecta*; water pennywort, *Hydrocotyl verticillata*; water speedwell, *Veronica anagalli aquatica*; dock, *Rumex verticillatus*; waterweed, *Elodea occidentalis*; and pondweed, *Potamogeton gramineus*; and algae such as *Rhizoclonium hieroglyphicum* and *Oscillatoria rubesens.*

METHODS

We measured density of *P. morrisoni* in the Oak Creek Springs Complex over four sampling periods during the summer of 2001. Initially, 35 modified Hester-Dendy artificial substrate samplers were placed randomly within the aquatic environment of accessible spring heads, spring runs, spring ponds, and spring pond outflows to quantify springsnail density. Artificial substrate samplers collect springsnails at densities comparable to those found in nearby natural substrata (O'Brien and Blinn, 1999). Samplers were constructed of round plates of masonite fastened together with an eye bolt. Each was composed of four round plates 75.49 mm in diameter and six round spacers 24 mm in diameter, all 1 cm thick, resulting in an effective sampling area of 330.86 cm^2 (Figure 2). Sampling periods were as follows: March 23 to May 10, May 10 to June 21, June 21 to August 2, and August 2 to September 25.

At the end of each sampling period, we used a Hydrolab Surveyor II to measure water temperature (°C), pH, dissolved oxygen (mg/L), and conductivity (µS/cm @ 25°C) adjacent to the sampler. We measured water depth with a meter stick or ruler (cm). We placed benthic fauna from each sampler into Whirl-Paks with 70% isopropyl alcohol or 95% ethyl alcohol, and transported them to the lab. We used a Stereozoom 7 Microscope to identify and count springsnails.

After data collection, we returned each sampler to the aquatic environment. Over the course of the four sampling periods, several samplers were unrecoverable. As a result, the initial 35 samplers provided 94 independent samples for each variable.

We classified substrate into one of four categories based on the predominant (>50%) composition surrounding the sampler. Substrate categories were modeled after a modified Wentworth classification system for particle size (Cummins, 1962; McMahon et al., 1996). Initially, we established three substrate categories with the following particle size range (mm): silt and sand (<2); gravel and pebble (2 to 64); and cobble (64 to 256). Later, we observed that in certain areas dominated by silt and sand, the leaf structure of water pennywort often provided a surface area atypical of other aquatic macrophytes. Accordingly, we split the silt and sand category into two sub-categories to capture potential differences provided by water pennywort. Those sub-categories are presented as silt and sand, and silt and sand with water pennywort.

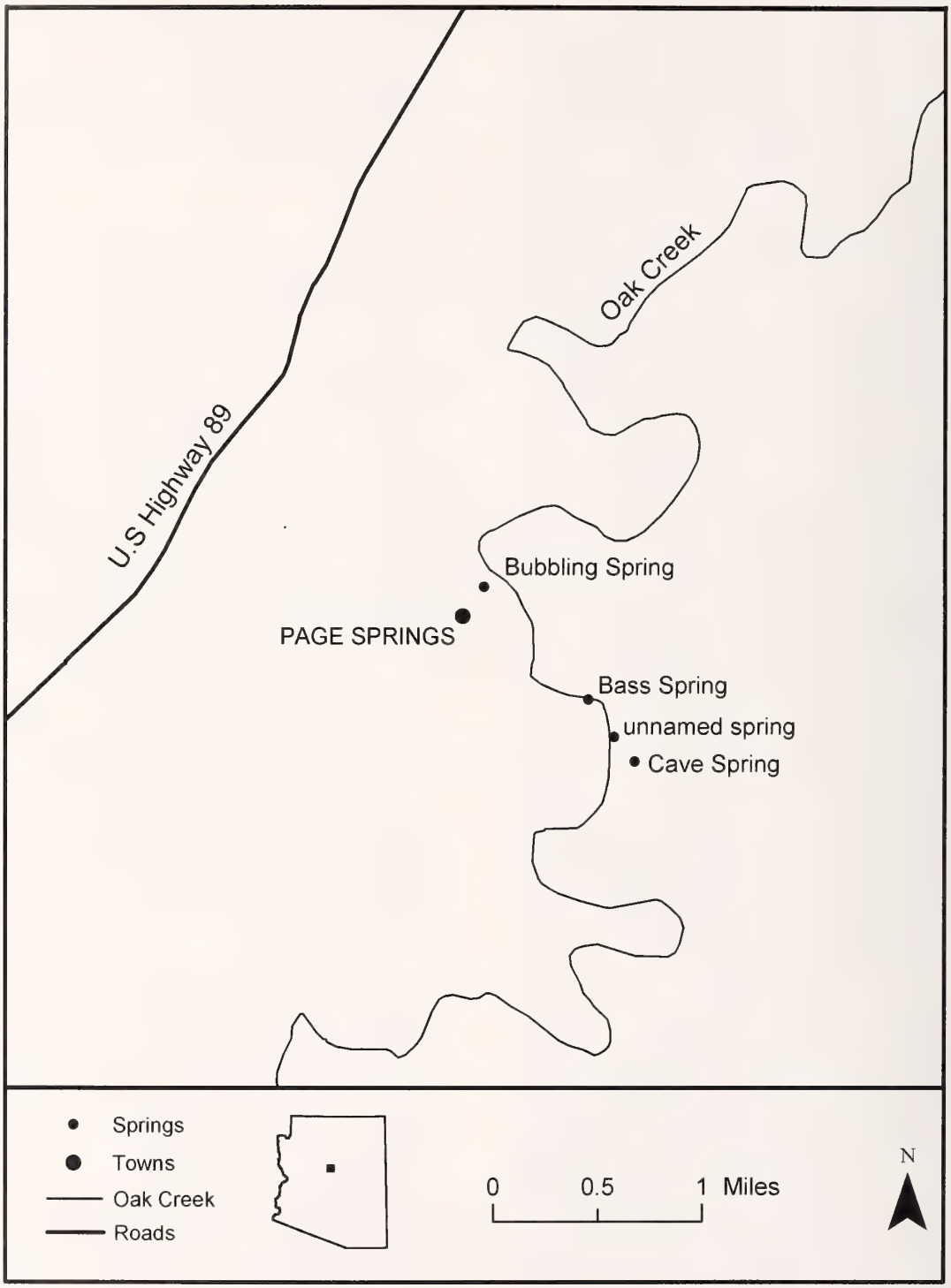


Figure 1. Page springsnail study area, Yavapai County, Arizona.

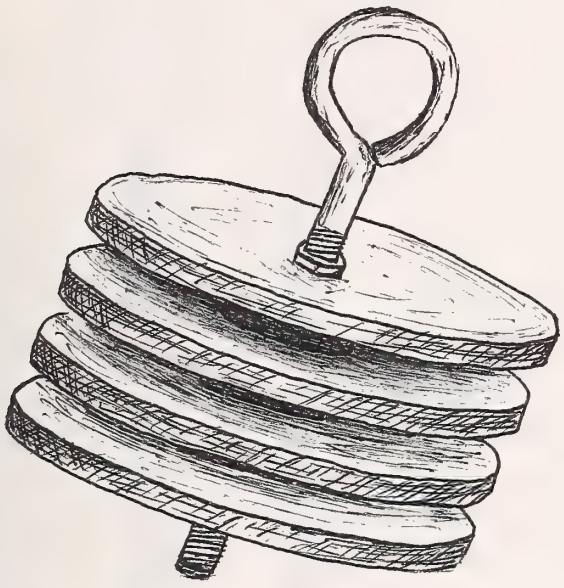


Figure 2. Modified Hester-Dendy artificial substrate sampler.

We did not encounter snails in the cobble category, largely because we did not collect a sufficient number of samples within cobbly areas (n = 6). Thus, for tests comparing snail density and presence between different substrate categories, we did not include the cobble classification.

Prior to statistical analyses, we used Pearson's correlation coefficients to evaluate the independence of pH, water temperature, dissolved oxygen, depth, and conductivity. Temperature and pH were correlated with dissolved oxygen ($r > 0.60$), and thus eliminated from further analyses. We kept dissolved oxygen instead of the former two variables because dissolved oxygen can be an important limiting factor for aquatic invertebrate respiration (Pennak, 1989). Moreover, although temperature differences as small as 4°C increased the production of viable freshwater snail eggs in other studies (Dillon, 2000), we do not suspect that temperature was a significant factor in our study since 96% of our temperature data varied less than 4°C.

Dissolved oxygen and conductivity were not highly correlated with one another ($r = 0.331$) and were both used as independent variables. Depth showed a fairly high correlation ($r = 0.564$) with conductivity, but the relationship between the two variables is unclear because our range of depth measurements did not appear broad enough to influence water quality through thermal stratification. Thus, depth was assessed along with the other independent variables. We pooled data between sampling periods, as a modified-Levene equal variance test showed the variances in snail density between periods to be equal ($F = 0.188$, df = 3, 90, $P = 0.904$) and there were no differences in snail densities between periods ($F = 0.13$, df = 3, 90, $P = 0.942$).

We pursued generalized tests, seeking differences in springsnail habitat between locations where springsnails were present and absent. We tested the following null hypotheses with respect to springsnail presence/absence: There is no difference according to substrate category, depth, dissolved oxygen levels, and conductivity levels.

We used a 3×2 contingency table to test whether snail presence was independent of substrate category, and Mann-Whitney *U*-tests to assess differences in habitat variables between occupied and unoccupied locations.

While our first hypotheses strove to characterize springsnail habitat in general, we also sought to characterize habitat quality by comparing snail densities among substrate categories, and between different levels of the continuous independent variables. We created low, medium, and high categories for each of the independent variables (dissolved oxygen, conductivity, and depth) using the lower, middle, and upper 33rd percentiles of data within the independent variables. Using these categories, we tested additional null hypotheses with respect to springsnail density: There is no difference according to substrate category, depth, dissolved oxygen, or conductivity.

We used the Kruskal-Wallis one-way ANOVA on ranks to test the above hypotheses, and the Kruskal-Wallis multiple comparison *z*-value test for post-hoc comparisons (Hintze, 2000).

NCSS (Hintze, 2000) was used for all statistical tests. We used nonparametric tests since the data generally lacked normality, and transformations were unsuccessful. For all tests, significance was considered $P \leq 0.05$ and results are presented in the form ($\bar{x} \pm$ SE).

RESULTS

For all 94 samples, springsnail density averaged 0.069 ± 0.0137 per cm^2, ranging from 0.0 to 0.680 per cm^2. We found springsnails in 48 samples, and where springsnails were found, their density averaged 0.135 ± 0.023 per cm^2. Throughout the study area (for locations with and without springsnails), dissolved oxygen levels averaged 8.694 ± 0.273 mg/L, ranging from 5.78 to 18.5 mg/L; conductivity levels averaged 431 ± 8.192 µS/cm, ranging from 128 to 524 µS/cm; and water depth averaged 28.225 ± 4.304 cm, ranging from 0.33 to 91.5 cm.

Defining Habitat Using Presence/Absence

Our contingency table analysis demonstrated that the occurrence of springsnails was not independent of substrate type (Table 1; $\chi^2 = 10.531$, df = 2, $P = 0.005$). The gravel/pebble category contained springsnails more often than expected, and both of the silt/sand categories contained springsnails less often than expected. Locations where springsnails were present were characterized by

Table 1

3 × 2 contingency table showing frequencies of Page springsnail presence and absence on three substrate categories during sampling in the Oak Creek Springs Complex in Arizona, 2001. Expected frequencies in parentheses.

Substrate	Absent	Present	Total
Gravel/pebble	14 (21.4)	33 (25.6)	47
Silt/sand	17 (11.4)	8 (13.6)	25
Silt/sand/water pennywort	9 (7.3)	7 (8.7)	16
Total	40	48	88

significantly lower dissolved oxygen levels (Figure 3A; $Z = -5.268$, $P < 0.0001$), lower conductivity levels (Figure 3B; $Z = -4.732$, $P < 0.0001$), and shallower depth (Figure 3C; $t = 2.135$, df = 41, $P = 0.039$).

Defining Habitat Quality Using Springsnail Density

Springsnail density differed between the three habitat substrates from which we sampled (Figure 4; $\chi^2 = 17.99$, df = 2, $P = 0.0003$). Springsnail density in gravel/pebble was significantly greater than in the silt/sand substrates (both with and without water pennywort). Springsnail density was lower for the highest level of dissolved oxygen (0.005 ± 0.005) compared to the lower two levels (Figure 5A; low = 0.084 ± 0.021; med = 0.069 ± 0.024; $\chi^2 = 26.49$, df = 2, $P < 0.0001$), lower for the highest two levels of conductivity than for the lowest level (Figure 5B; low = 0.124 ± 0.029; med = 0.020 ± 0.010; high = 0.013 ± 0.008; $\chi^2 = 30.32$, df = 2, $P < 0.0001$), and remained unchanged for all levels of water depth (Figure 5C; shallow = 0.074 ± 0.003; med = 0.083 ± 0.037; deep = 0.036 ± 0.019; $\chi^2 = 2.83$, df = 2, $P = 0.242$).

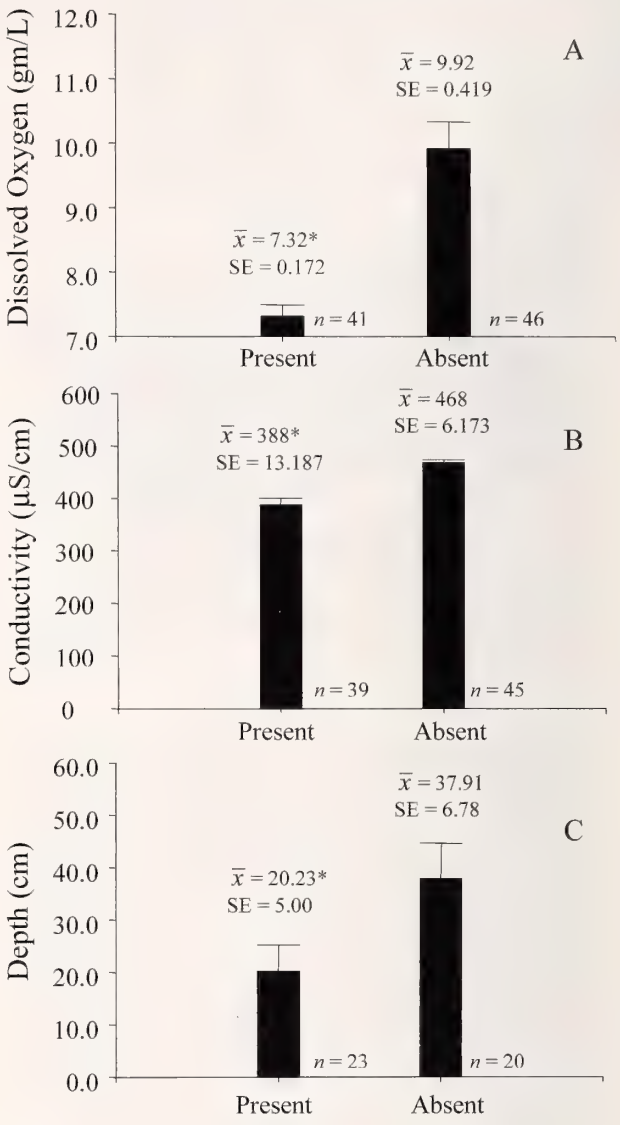


Figure 3. Mean values for three habitat parameters where Page springsnail was present and absent in the Oak Creek Springs Complex in Arizona, 2001. Differences were tested with Mann-Whitney *U*-tests comparing sites with and without springsnails. *$P < 0.05$.

DISCUSSION

We found that substrate particle size was an important factor determining occurrence and density. *P. morrisoni* occurred more often and in greater densities in gravel and pebble substrates. They may prefer larger substrate because it provides a reliable surface for the deposition of egg masses, facilitates mobility, and provides a suitable medium for production of periphyton, the snails' preferred food source. This, in turn, may result in higher recruitment and snail densities.

Mladenka (1992) demonstrated that *P. bruneauensis* preferred gravel to sand because snails used hard surfaces to deposit their eggs. *Pyrgulopsis* females deposit single, small egg capsules on hard surfaces (Hershler, 1998). Larger substrates should be more conducive to oviposition because the surface provides improved stability over smaller, uncoalesced particles such as silt and sand. Moreover, prosobranch snails have a distinct foot with a creeping planar sole and locomotion is facilitated by secretion of a mucous trail over which the animal glides (Brusca and Brusca, 1990). This type of locomotion likely requires less effort over large and stable surfaces. Smaller particles are also more likely to be displaced by water current, possibly burying snails and eggs.

We did not include cobble within our analysis because our sample size in that category was small. However, we

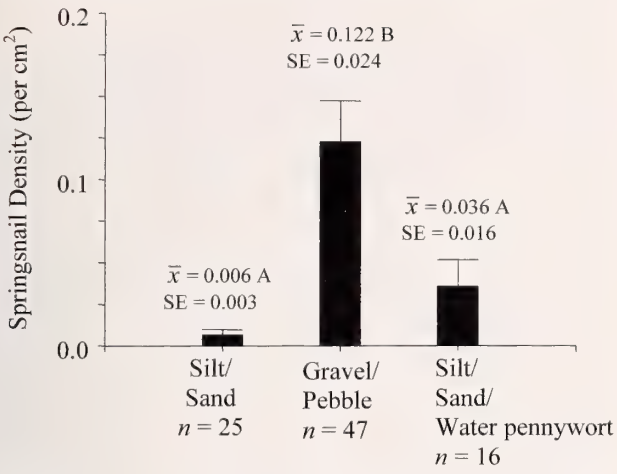


Figure 4. Values for Page springsnail density ($\bar{x} \pm$ SE) in three different substrate types in the Oak Creek Springs Complex in Arizona, 2001. Means with the same letter did not differ when tested with a Kruskal-Wallis one-way ANOVA on ranks at α = 0.05.

do not dismiss cobble as a potentially preferred substrate medium due to its large, stable character. *P. morrisoni* did not show a significant preference for water pennywort as a substrate medium. We found this surprising since anecdotal field observations convinced us that the species was abundant on the leaves of water pennywort. Upon reflection, perhaps our sampling technique did not capture the importance of water pennywort as a substrate medium.

Water pennywort occurred within only one spring that we sampled. That spring, Bubbling Spring, is not a rheocrene, but instead exists as a pond with a maximum measured depth of 91.5 cm. Within Bubbling Spring pond, water pennywort occurred near spring vents and grew to a height of about 15–20 cm within the water column. Because samplers were placed in sediments near the stem base, the snail population present on the leaves may not have been able to access them. Perhaps this could be addressed by using the surface area of the macrophyte itself to quantify snail density as done by O'Brien and Blinn (1999).

Nevertheless, we believe the potential suitability of water pennywort as a substrate medium for *P. morrisoni* deserves further investigation. A substrate-stratified field sampling technique or laboratory experiment may be useful to assess the importance of all substrate types.

We found that mean dissolved oxygen concentrations differed by more than 2 mg/L in sites where springsnails were present versus sites where springsnails were absent. Moreover, regions with high dissolved oxygen concentrations had significantly lower snail densities than sites with low and medium concentrations. We do not suspect that depressed dissolved oxygen levels limited respiration because we never encountered oxygen-poor conditions (minimum value = 5.78 mg/L). For common species of the pulmonate genus *Physella,* 2 mg/L is about the limiting level for dissolved oxygen to meet respiratory needs (Pennak, 1989). However, we have no reason to postulate that higher levels of dissolved oxygen would directly limit *P. morrisoni* occurrence and density, given that higher levels should more readily meet respiratory requirements. Thus, the negative relationship between dissolved oxygen and snail occurrence and density may be a function of

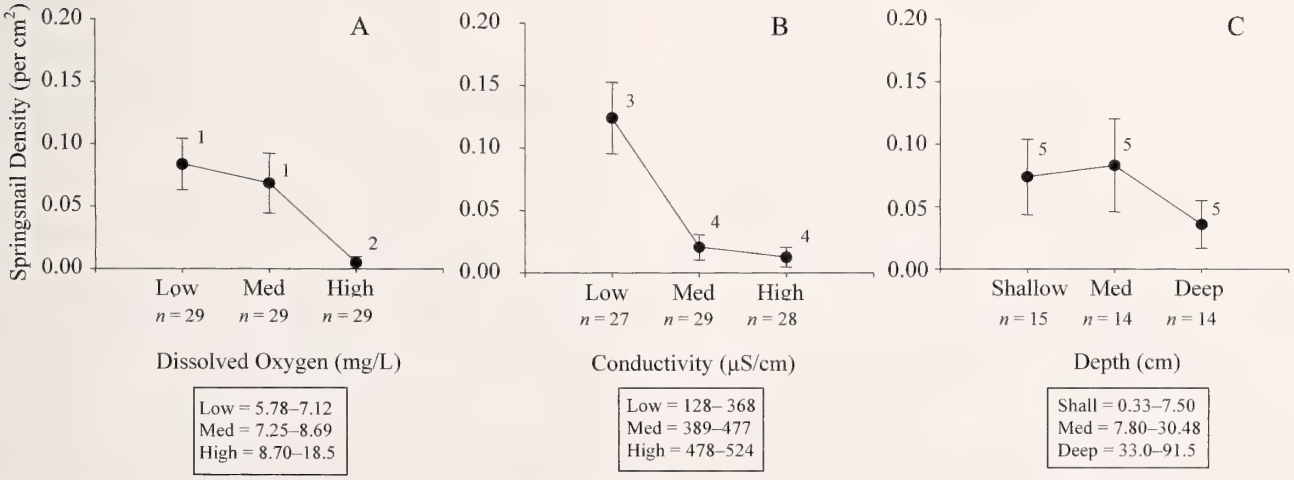


Figure 5. Values for Page springsnail density ($\bar{x} \pm$ SE) in relation to three different environmental variables in the Oak Springs Complex in Arizona, 2001. Values with same number did not differ when tested with a Kruskal-Wallis one-way ANOVA on ranks at α = 0.05. Low, medium, and high categories were created using the lower, medium, and upper 33rd percentiles of data within the independent variables.

other environmental variables that interact with both dissolved oxygen and the snail. These may include the influence of other gases and/or primary productivity.

For instance, it is generally true that dissolved oxygen and carbon dioxide concentrations exhibit an inverse relationship within aquatic environments. Coupled with sunlight, carbon dioxide is the primary element driving photosynthesis. It is possible that regions within the Oak Creek Springs Complex characterized by low dissolved oxygen levels were also characterized by elevated levels of carbon dioxide and primary production, particularly at the periphytic level. Perhaps the relationship between dissolved oxygen and occurrence and density of *P. morrisoni* is tied to the availability of periphyton.

Whatever the mechanism, the proximity of spring vents may play an important role. Hershler (1984, 1998) noted that hydrobiid densities seem to decrease downflow from spring sources. Although our design was not structured to capture this influence, it is important to note that *P. morrisoni* seemed most abundant near spring vents, particularly within Bubbling Spring pond. If dissolved oxygen concentrations nearer spring vents were lower than concentrations away from vents, and springsnails were most abundant near spring vents, we would expect a negative relationship between springsnail abundance and dissolved oxygen. An ad-hoc analysis showed that sampling stations within 10 m of spring vents in Bubbling Spring pond had a mean dissolved oxygen concentration of 7.27 $\pm$ 0.127 mg/L while stations greater than 10 m from vents had a mean concentration of 10.77 $\pm$ 2.79 mg/L (t = 7.17, df = 38.6, $P < 0.0001$). This relationship closely resembles the results of our tests for snail presence and density.

We therefore have reason to believe that dissolved oxygen concentrations and occurrence and density of *P. morrisoni* were heavily influenced by proximity to spring vents. Regions nearer spring vents may provide environmental conditions that better meet the species' physiological need. This may be tied to geologic and ecological subterranean processes that determine the nature of water quality near vents. Another factor may be significant diel fluctuations in water quality. Perhaps water further from spring vents exhibits greater variability in extreme conditions due to atmospheric influences while water closer to vents is more stable. A sampling methodology designed to capture the influence of diel fluctuations could provide important insight.

We found differences in mean conductivity concentrations in locations where the species was present versus locations where the species was absent. Sites with high and medium levels of conductivity had lower snail densities than sites with low conductivity levels.

Conductivity is commonly used as an index of dissolved solids, particularly salts. Salts can play a major role in determining mollusk population density and distribution because they are used in shell formation (Pennak, 1989). Though we find the relationship perplexing, lower levels of conductivity seem to be preferred by *P. morrisoni.* Perhaps lower levels of dissolved salts are more readily assimilated. Or, as with dissolved oxygen, perhaps the relationship is tied to other factors, such as proximity to spring vents and their associated stable environmental conditions.

We found that water depth influenced *P. morrisoni* occurrence, and mean water depth was greater in regions where the species was absent versus regions where present. Although depth did not appear to influence springsnail densities, deeper sites had non-significantly lower snail densities than sites with shallow and medium depths. A larger sample size may have shown this definitively.

Water depth can substantially influence aquatic ecosystems. Sunlight can more readily penetrate shallower regions, raising water temperature and boosting photosynthetic rates. Deeper waters are more accessible to a diverse assemblage of organisms, such as fishes, that may act as predators. Although we did not attempt to assess the effect of predation, it is important to note that occurrence and density of aquatic mollusks can be greatly influenced by the presence of predators, particularly fishes.

Experiments conducted by Myler (2000) showed that redbelly tilapia (*Tilapia zilli*) significantly reduced the food availability for *P. bruneauensis* and tilapia actively ate individual snails they encountered. Raisanen (1991) reported shells of *P. morrisoni* in a gut analysis of mosquitofish (*Gambusia affinis*) from Bubbling Spring. The potential influence of water depth on the abundance and foraging habits of predaceous fishes within the Oak Creek Springs Complex deserves more attention.

Our study constitutes the first empirical effort to define *P. morrisoni* habitat and should prove useful in assessing the relative suitability of natural or restored spring environments for the species. It is important, however, to view the structure of an aquatic ecosystem as a complex web of intricate relationships between various biotic and abiotic variables. Benthic organisms can be affected by a multitude of variables, most of which are extremely difficult, if not impossible, to manipulate or control. As such, caution should be used when actively managing spring environments to provide suitable habitat for endemic invertebrates.

Since it is reasonable to conclude that snail density is indicative of habitat quality (cf. Van Horne, 1983), we recommend that management actions focus on providing preferred substrates and water depths. This may be accomplished by ensuring the physical environment facilitates water velocities that promote the maintenance of gravel and pebble substrates. Specifically, the shear stress of flowing water should effectively transport fine sediments out of the system. A rheocrene environment should provide the most appropriate substrate medium and may serve to boost snail recruitment and density.

Although managing water chemistry variables at levels that promote occupancy and high density would be difficult, our results can be used to assess the relative suitability of a spring for the species. This may have practical application for possible reintroduction or transplantation efforts. Until now, little information was available to judge the suitability of sites considered for reintroduction or transplantation.

Directly manipulating dissolved oxygen and conductivity in a spring to levels most conducive to *P. morrisoni* occupancy and high density would probably be impractical. Such efforts would likely be costly with low success rates. As such, we suggest the best approach to provide habitat is to maintain springs in their natural rheocrene condition. This is consistent with Hershler and Williams (1996) who suggested that efforts to maintain springsnail populations should focus on the maintenance of natural spring head integrity, which will improve water quality and conserve springsnails.

Acknowledgments. We thank the Arizona Game and Fish Department for granting access to springs located on their property. We thank the following individuals for their contribution to this manuscript: Linda Allison, Winnie Chen, Mike Demlong, Mima Falk, Tom Gatz, Steven Goldsmith, Kathy Goodhart, Ryan Gordon, Jennifer Graves, David Harlow, Suzie Hatten, Carrie Marr, Don Metz, Clay Nelson, Mary Richardson, Don Sada, Jeff Sorensen, Roger Sorensen, Larry Stevens, Jerry Stefferud, Sally Stefferud, Arlene Tavizon, and three anonymous reviewers.

LITERATURE CITED

Arizona Game and Fish Department. 1988. Environmental assessment, Page Springs hatchery renovation. Prepared by Planning and Evaluation Branch, Special Services Division and Fisheries Branch, Wildlife Management Division. 78 pp.

Brusca, R. C. & G. J. Brusca. 1990. Invertebrates. Sinaur Associates, Inc.: Sunderland, Massachusetts. 922 pp.

Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. American Midland Naturalist 67:477–504.

Dillon, R. T. 2000. The Ecology of Freshwaters. Cambridge University Press. 509 pp.

Dundee, D. S., P. H. Phillips & J. D. Newsom. 1967. Snails on migratory birds. The Nautilus 80(3):89–91.

Greeson, P. E. 1982. Why biology in water-quality studies? Pp. A3–A5 in P. E. Greeson (ed.), Biota and Biological Principles of the Aquatic Environment. Geological Survey Circular 848-A.

Hendrickson, D. A. & W. L. Minckley. 1984. Ciénegas-vanishing climax communities of the American Southwest. Desert Plants 6(3):130–175

Hershler, R. 1984. The hydrobiid snails (Gastropoda: Rissoacea) of the Cuatro Cienegas basin: systematic relationships and ecology of a unique fauna. Journal of the Arizona–Nevada Academy of Science 19:61–76.

Hershler, R. 1990. *Pyrgulopsis bruneauensis,* a new springsnail (Gastropoda: Hydrobiidae) from the Snake River Plain, southern Idaho. Proceedings of the Biological Society of Washington 103:803–814.

Hershler, R. 1994. A review of the North American freshwater snail genus *Pyrgulopsis* (Hydrobiidae). Smithsonian Contributions to Zoology, Number 554. 52 pp.

Hershler, R. 1998. A systematic review of the hydrobiid snails (Gastropoda: Rissooidea) of the Great Basin, western United States. Part I. Genus *Pyrgulopsis.* The Veliger 41(1):1–132.

Hershler, R. & J. J. Landye. 1988. Arizona Hydrobiidae (Prosobranchia: Rissoacea). Smithsonian Contributions to Zoology, Number 459. 63 pp.

Hershler, R. & J. E. Williams. 1996. Conservation strategies for springsnails in the Great Basin: the challenge and the opportunities. Proceedings of the Desert Fishes Council, 1995 Symposium. XXVII. 1 p.

Hintze, J. L. 2000. NCSS 2000. Statistical system for Windows. Vol. 1-3. NCSS: Kaysville, Utah, USA.

Landye, J. J. 1973. Status of the inland aquatic and semi-aquatic mollusks of the American southwest. Report submitted to U.S. Department of Interior, Bureau of Sport Fisheries and Wildlife, Office of Rare and Endangered Species, Washington, D.C. 60 pp.

Landye, J. J. 1981. Current status of endangered, threatened, and/or rare mollusks of New Mexico and Arizona. A report submitted to the U.S. Department of Interior, Bureau of Sport Fisheries and Wildlife, Office of Rare and Endangered Species, Albuquerque, New Mexico. 35 pp.

McMahon, T. E., A. V. Zale & D. J. Orth. 1996. Aquatic habitat measurements. Pp. 83–120 in B. R. Murphy & D. W. Willis (eds.), Fisheries Techniques. 2nd ed. American Fisheries Society: Bethesda, Maryland.

Mladenka, G. C. 1992. The ecological life history of the Bruneau Hot Springs snail *Pyrgulopsis bruneauensis.* Final Report. Stream Ecology Center. Department of Biological Sciences. Idaho State University. 116 pp.

Mladenka, G. C. & G. W. Minshall. 2001. Variation in the life history and abundance of three populations of Bruneau Hot springsnails *Pyrgulopsis bruneauensis.* Western North American Naturalist 61(2):204–212.

Myler, C. D. 2000. Habitat improvement for an endangered springsnail in southwest Idaho. M.S. Thesis, Idaho State University. 45 p.

New, T. R. 1998. Invertebrate Surveys for Conservation. Oxford University Press. 240 pp.

O'Brien, C. & D. W. Blinn. 1999. The endemic spring snail *Pyrgulopsis montezumensis* in a high CO_2 environment: importance of extreme chemical habitats as refugia. Freshwater Biology 42:225–234.

Pennak, R. W. 1989. Freshwater Invertebrates of the United States: Protozoa to Mollusca. John Wiley and Sons, Inc.: New York. 628 pp.

Raisanen, C. 1991. Status survey of four invertebrates of the Page/Bubbling/Lolomai springs/Oak Creek complex. A report prepared for USDI Fish and Wildlife Service, Albuquerque, New Mexico. 106 pp.

Taylor, D. W. 1987. Fresh-water molluscs from New Mexico and vicinity. New Mexico Bureau of Mines and Minerals 116:1–50.

U.S. Fish and Wildlife Service. 2004a. Endangered Species Bulletin. U.S. Department of the Interior, Fish and Wildlife Service. Washington D.C. XXIX(2). 43 pp.

U.S. Fish and Wildlife Service. 2004b. Endangered and Threatened Wildlife and Plants; Review of Species That Are Candidates or Proposed for Listing as Endangered or Threatened; Annual Notice of Findings on Resubmitted Petitions;

Annual Description of Progress on Listing Actions; Notice of Review; Proposed Rule. Federal Register 69(86):24876–24904.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Williams, J. E., D. B. Bowman, J. E. Brooks, A. A. Echelle, R. J. Edwards, D. A. Hendrickson & J. J. Landye. 1985. Endangered aquatic ecosystems in North American deserts with a list of vanishing fishes of the region. Journal of the Arizona–Nevada Academy of Science 20:1–62.

The Veliger 48(1):17–25 (June 30, 2006)

THE VELIGER

A Light and Electron Microscopic Study of Pigmented Corpuscles in the Midgut Gland and Feces of *Pomacea canaliculata* (Caenogastropoda: Ampullariidae)

EDUARDO KOCH,* ISRAEL A. VEGA,* EDUARDO A. ALBRECHT*

Laboratory of Physiology (IHEM-CONICET), Department of Morphology and Physiology, University of Cuyo, Casilla de Correo 33, M5500 Mendoza, Argentina

HUGO H. ORTEGA

Laboratorio de Endocrinología y Tumores Hormonodependientes (LETH-UNL); present address: Laboratorio de Investigaciones Histológicas Aplicadas (FCV-UNL), Santa Fe, Argentina

AND

ALFREDO CASTRO-VAZQUEZ

Laboratory of Physiology (IHEM-CONICET), Department of Morphology and Physiology, University of Cuyo, Casilla de Correo 33, M5500 Mendoza, Argentina

Abstract. Pigmented corpuscles (C and K types) and their cellular associations in the midgut gland, as well as similar pigmented corpuscles in snail's feces and in up to 3-year-old aquarium sediments, were studied. C corpuscles are light brown-greenish spherical bodies (diameter 14 μm) surrounded by a thick, electron dense wall, and containing inner granules and membranes. A rather large variation in the amount of these granules and membranes occurs in C corpuscles, irrespective of whether they were from gland tissue, feces or aquarium sediments. K corpuscles are dark brown, bottle-shaped bodies (36 μm length, 14 μm width) which frequently show a multilamellar structure. All transitional forms between typical C and K corpuscles occur. K corpuscles occur more frequently than C corpuscles in gland tissue but not as much in feces, and are even less frequent in old aquarium sediments. Glandular C corpuscles are contained within vesicles of alveolar columnar cells, and they occur mainly in the basal half of these cells. In the cellular upper half, similar but nude (i.e., without the wall) bodies are seen. On their part, glandular K corpuscles are apparently contained within an extrusion of a columnar cell, which is in turn engulfed by a pyramidal cell. Morphological features of K corpuscles and of their hosting cells indicate that K corpuscles derive from C corpuscles and that the hosting cells partly provide their electron dense layers. Interestingly, the amount of pigmented materials in the midgut gland of females is more than double than that of males.

INTRODUCTION

Andrews (1965) published a brief account of the histology of the midgut gland of *Pomacea canaliculata* (Lamarck, 1822), noticing the existence of two distinct types of intracellular pigmented corpuscles that were freed from glandular cells, and were embedded in what she called the "liver string": a continuous mucous string that was to mix in the gut with the intermittent "gastric string" of partly digested food. She referred to these corpuscles as "greenish spherules" and "brown concretions" (we have referred to them as C and K corpuscles, respectively; Castro-Vazquez et al., 2002).

Andrews (1965) also ascribed, on morphological grounds, a digestive-excretory function to C corpuscles and an excretory function to K corpuscles. However, since C corpuscles in the liver string are each packed into a rather thick envelope, and appear as such in the feces, their possible role as carriers of digestive enzymes for extracellular digestion seemed questionable. The present study reexamines the morphology of these corpuscles, as part of a broader program to disclose the nature of these quantitatively important components of the midgut gland.

MATERIAL AND METHODS

Animals

Individuals of *P. canaliculata* were either collected in the Rosedal Lake (Palermo Park, Buenos Aires, Argentina) or were laboratory-born descendants from them. Voucher, alcohol-preserved specimens of the original population and of the cultured animals were deposited in

* These authors have contributed equally to this work.

the collection of the Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina; lots MACN-In 35707 and MACN-In 36046, respectively). They were kept in indoor aquaria, under constant temperature (24°C) and day length (14 hr light and 10 hr dark), and fed with lettuce, supplemented with calcium carbonate. Shell lengths ranged from 30 to 50 mm.

Light and Electron Microscopy

Fecal droppings of different sizes and shapes were collected soon after deposition, and were either studied directly under light microscopy or prepared for electron microscopy (see below). Also, sediment samples taken from aquaria containing *P. canaliculata* were studied after varying periods (1–36 months) after sampling.

Light microscopy preparations were obtained from 5 males and 5 females by cutting 1–2 mm thick slices of the midgut gland with a razor blade from the gland's surface, close to the kidney's boundary. The samples were fixed in dilute Bouin's fluid for one week at 4°C. Then, they were placed in 70% ethanol, subsequently dehydrated, embedded in paraffin and sectioned (5 μm). Separate sections were stained with either Harris hematoxylin-eosin or iron hematoxylin (Clark, 1981).

Digital micrographs (24 bit color format, 640 × 480 pixels) were obtained with a color video camera on a microscope. Morphometric analyses were made using Image Pro-Plus 3.0® (Media Cybernetics, Silver Spring, MA, USA) on iron hematoxylin preparations of midgut glands obtained from 5 animals of both sexes (25–50 slides were analyzed per animal). If no sexual differences were apparent, data from both sexes were pooled for presentation. However, a sexual difference was apparent in the relative abundance of C and K corpuscles in iron hematoxylin preparations. This difference was quantified as the percent of surface occupied by pigmented areas in unstained preparations from both males and females. For this purpose, color segmentation in the chromatic range of both C and K corpuscles was made on 35 microscopical fields (0.334 mm^2 each) of unstained slides from 4 males and 4 females; the surface occupied by the darker areas of C corpuscles (see Results) was separated from that occupied by K corpuscles by filtering pigmented areas smaller than 30 μm^2. Differences between means were analyzed with Student's *t* test.

Also, the glands of adult individuals were processed for electron microscopy. Small pieces of the gland were fixed in 2.5% glutaraldehyde buffered with 0.1 M phosphate (pH 7.4) and postfixed in 1% osmium-tetroxide and 2% uranyl acetate. Later they were dehydrated in a graded series of ethanol and acetone, embedded in Spurr's resin, and sectioned with a diamond knife. Ultrathin sections were stained with uranyl acetate and lead citrate and examined in a transmission electron microscope. For topographic orientation, 1 μm sections were stained with 1% toluidine blue.

RESULTS

General Characteristics of C and K Corpuscles

C corpuscles are greenish/light brown spheres (Figure 1B) that usually contain darker, more or less rounded condensations of varying sizes. In general, their light microscopical appearance is similar whether they are obtained from midgut gland tissue, feces or aquarium sediments (up to three years after sampling). However, some distortion of C corpuscles in these sediments may be occasionally observed (see below).

Transmission electron microscopy revealed they are lined by an electron-dense wall (Figure 3). Sometimes, an outer membrane is seen detached from the external wall (Figure 4A, B). These corpuscles contain very fine to coarse granules (Figure 3); coarse granules are mostly associated in clusters that seemingly correspond to the pigmented condensations seen in fresh material. Also, there are irregular inner membranes that are not associated with granules. The relative abundance of these components is variable among different corpuscles, but this variation cannot be correlated to the origin of the corpuscles (feces, aquarium sediments or midgut gland samples).

K corpuscles in fresh material (Figure 1C) are dark brown, bottle or club-shaped bodies. Even though most of them are opaque, some appear composed of multiple, concentric lamellae in which a group of several small, rounded bodies are embedded. Besides those typical K corpuscles there are also corpuscles that appear intermediate between C and K corpuscles (Figure 1C).

K corpuscles are very abundant in glandular tissue but not in feces or aquarium sediments. Under the electron microscope they appear as either compact or multilamellar electron dense bodies (Figure 5) but we have not been able to obtain suitable sections of the inner core of these hard bodies, probably because the embedding resin was not able to adequately penetrate them.

C and K Corpuscles in Fecal Droppings and Aquarium Sediments

Two types of fecal droppings compose the snail's fecal stream: (a) sticky strings of thin oval droppings (less than 1 mm thick and several mm in length), and (b) larger fecal droppings of irregular shape (around 1 mm thick and up to 3 mm long) and not adherent to each other.

The thin and sticky strings are composed of only C and K corpuscles (their relative proportions may vary, but C corpuscles are always more abundant than K corpuscles) embedded in a mucous matrix. These strings (Figure 1A) appear similar to what Andrews (1965) described as the "liver string." The larger fecal droppings were composed

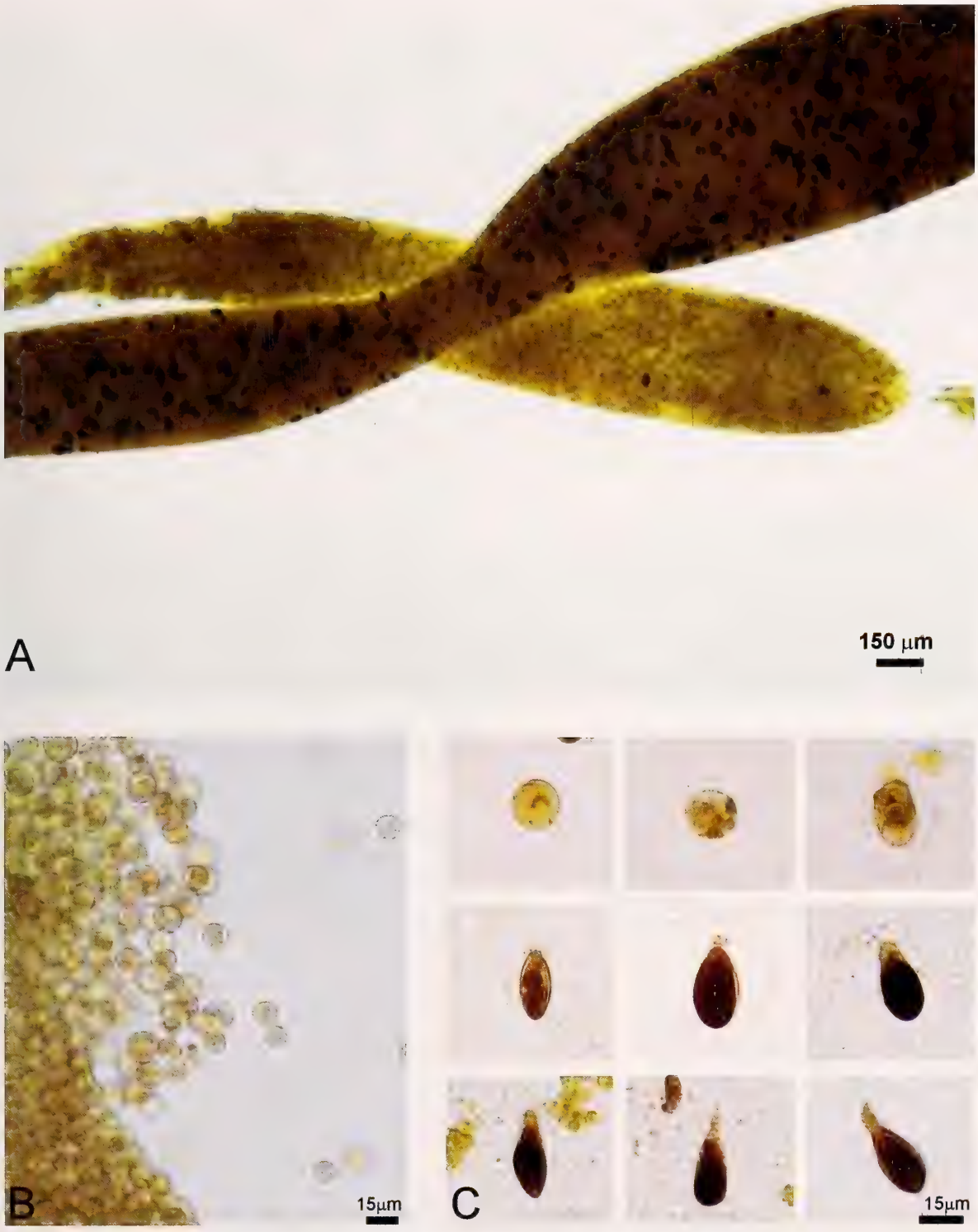


Figure 1. **A.** Two unstained strings of fecal droppings, mainly composed of C corpuscles embedded in a mucous matrix; many darker and larger K corpuscles are seen in the darker string. **B.** Unstained C corpuscles from a fecal dropping composed of C corpuscles only. **C.** Unstained glandular corpuscles ranging from the typical C type to the typical K type.

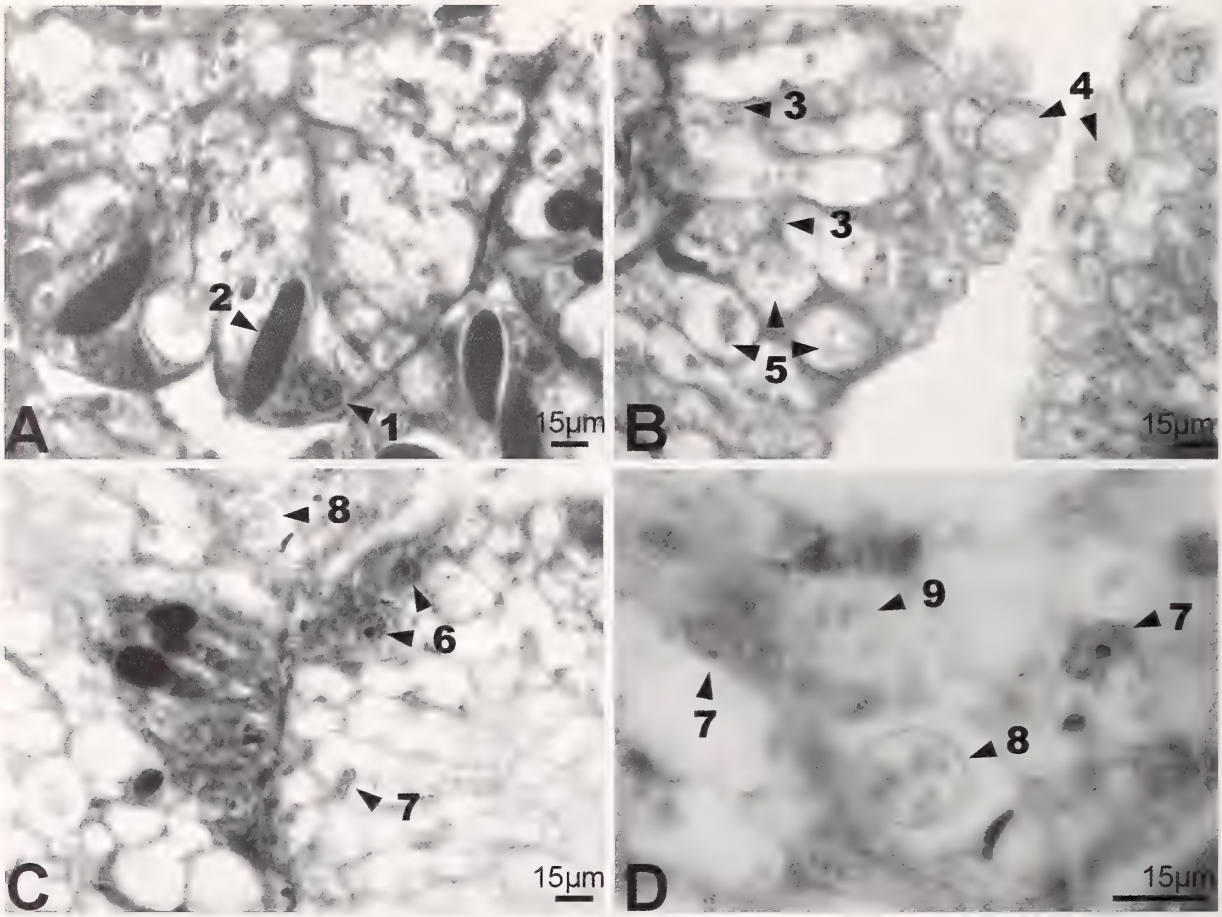


Figure 2. Midgut gland alveolar cells associated with C and K corpuscles (iron hematoxylin, scale bars = 15 µm). **A.** A pyramidal cell, with a large basophilic cytoplasm and a basal nucleus [1], with a prominent nucleolus. An elongated K corpuscle [2] appears contained within the pyramidal cell's cytoplasm. **B.** Columnar cells, with small nuclei and nucleoli [3], showing apical bodies [4], probably nude C corpuscles that are being extruded into the gland's lumen; large cytoplasmic vesicles contain a granular, basophilic material [5]. **C.** An alveolus showing basophilic cells with large nuclei [6], as well as columnar cells with small nuclei [7] and a clear vesicular cytoplasm; a walled C corpuscle is seen as a distinct spherule containing inner condensations, probably at the base of another alveolus [8]. **D.** Higher magnification of the same C corpuscle [8], showing its distinct limits (the wall and the darkly stained inner condensations; similar material is contained in a less distinct spherule [9] which may be a nude C corpuscle; columnar cells nuclei [7] are seen in the surrounding region.

of digested food remnants of varying size and appearance, and they also contained C and K corpuscles in varying amounts.

The sizes of C and K corpuscles were measured in fresh fecal strings (obtained from 7 animals, 25 corpuscles per animal were measured). The outer diameter of C corpuscles in the liver string was 13.7 ± 0.4 µm (results of this and all subsequent measurements are expressed as mean ± SEM). The length and width of K corpuscles were determined by measuring the rectangles inscribing them (length and width were 35.6 ± 1.1 µm and 13.5 ± 0.4 µm, respectively).

The external shape of some C corpuscles in aquarium sediments was sometimes distorted, adopting semilunar or even more irregular shapes.

Cellular Associations of C and K Corpuscles in the Midgut Gland

The gland of *P. canaliculata* is composed of elongated irregular alveoli (135.6 ± 0.6 µm in diameter), the epithelium of which (60.8 ± 0.6 µm in height) is formed by two cell types (pyramidal and columnar) that line a lumen of irregular width (Figure 2A–C).

Columnar cells appear in iron hematoxylin preparations as vesicle containing cells, with a rather small nucleus (4.9 ± 0.4 µm in diameter) and a nucleolus. Generally, the nucleus is placed laterally, in the lower half of the cell. As noted by Andrews (1965), the height of columnar cells is similar in all the alveoli of the same individual, but it varies among individuals, what that author

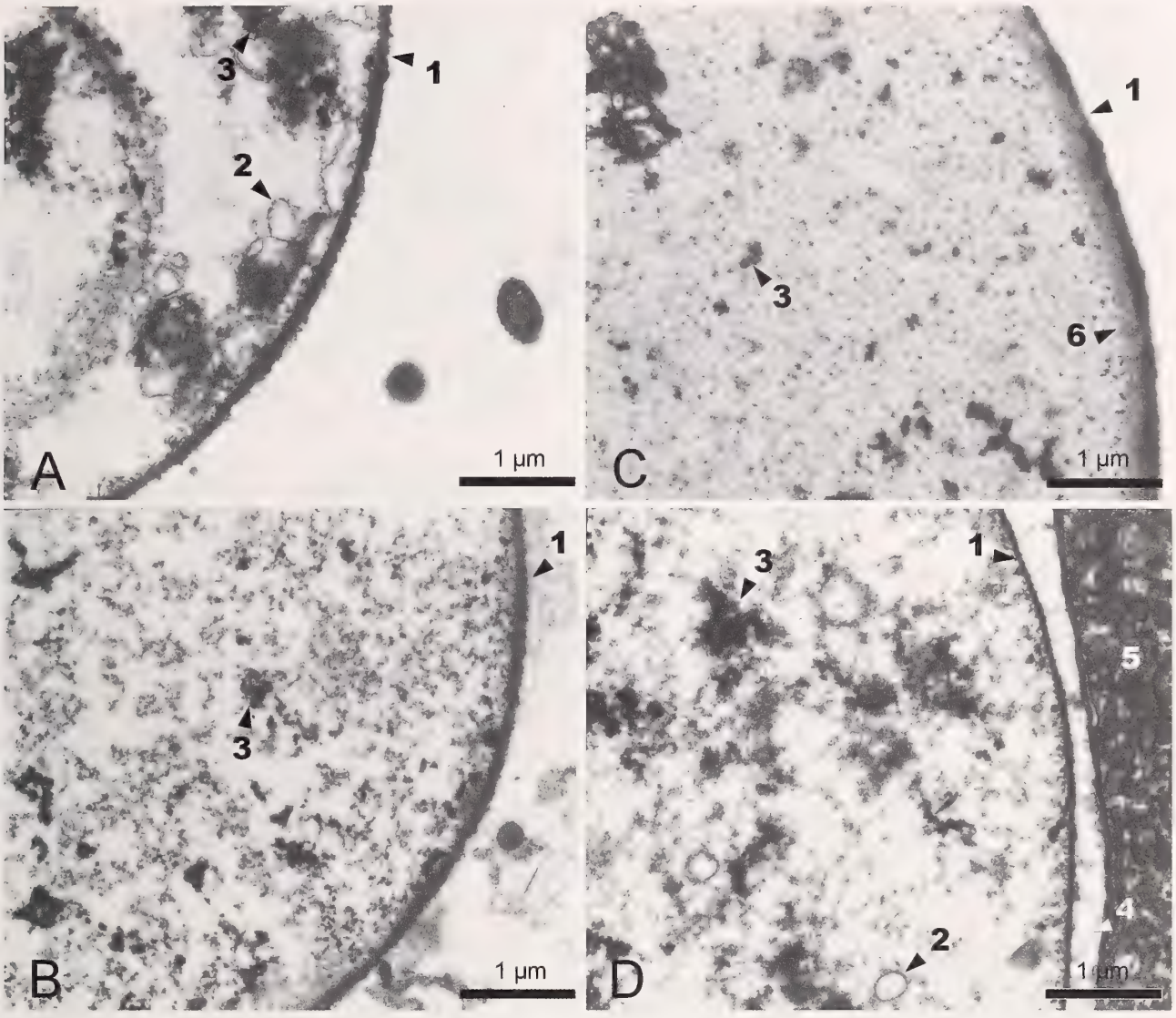


Figure 3. Electron micrographs (scale bars = 1 µm) of extra- and intracellular C corpuscles. **A.** C corpuscle in a fecal dropping; the nearby small electron dense bodies are cocci. **B.** C corpuscle in a 36-month-old aquarium sediment. **C.** A more dense C corpuscle in the same old aquarium sediment. **D.** C corpuscle contained within a glandular cell. [1] outer wall; [2] inner membranes; [3] coarse granules; [4] vesicle surrounding the corpuscle; [5] glandular cell cytoplasm; [6] condensation of fine granules below the outer wall.

attributed to different functional digestive or excretory states.

When the cells are high, their apex is frequently dome-shaped, and clear globules or vesicles appear protruding into the lumen, as if a process of apocrine secretion was going on (Figure 2B). Sometimes the vesicles appear empty (Figure 2C), especially when iron hematoxylin preparations are thoroughly differentiated. However, in many cases, they appear filled with stainable material of varying appearance (Figure 2A, B). In many other cases, particularly in the basal third of the epithelial cells, the corpuscle contained within the vesicle appears surrounded by a wall (Figure 2C, D); these walled corpuscles are frequently pigmented (greenish/brownish in color) and can be recognized even in unstained preparations. The walled, pigmented corpuscles seem identical to fecal C corpuscles, because of their appearance, color and size (outer diameter µm of corpuscle-containing vesicles was 12.3 ± 0.4).

Electron microscopy of the basal region of the columnar cells shows many C corpuscles (Figure 3) each surrounded by an electron-dense wall and contained within a large vesicle. Their inner structure is in all respects similar to that of C corpuscles in either feces or sediments. Along with the walled C corpuscles, other membrane-bound bodies of variable size and content (similar

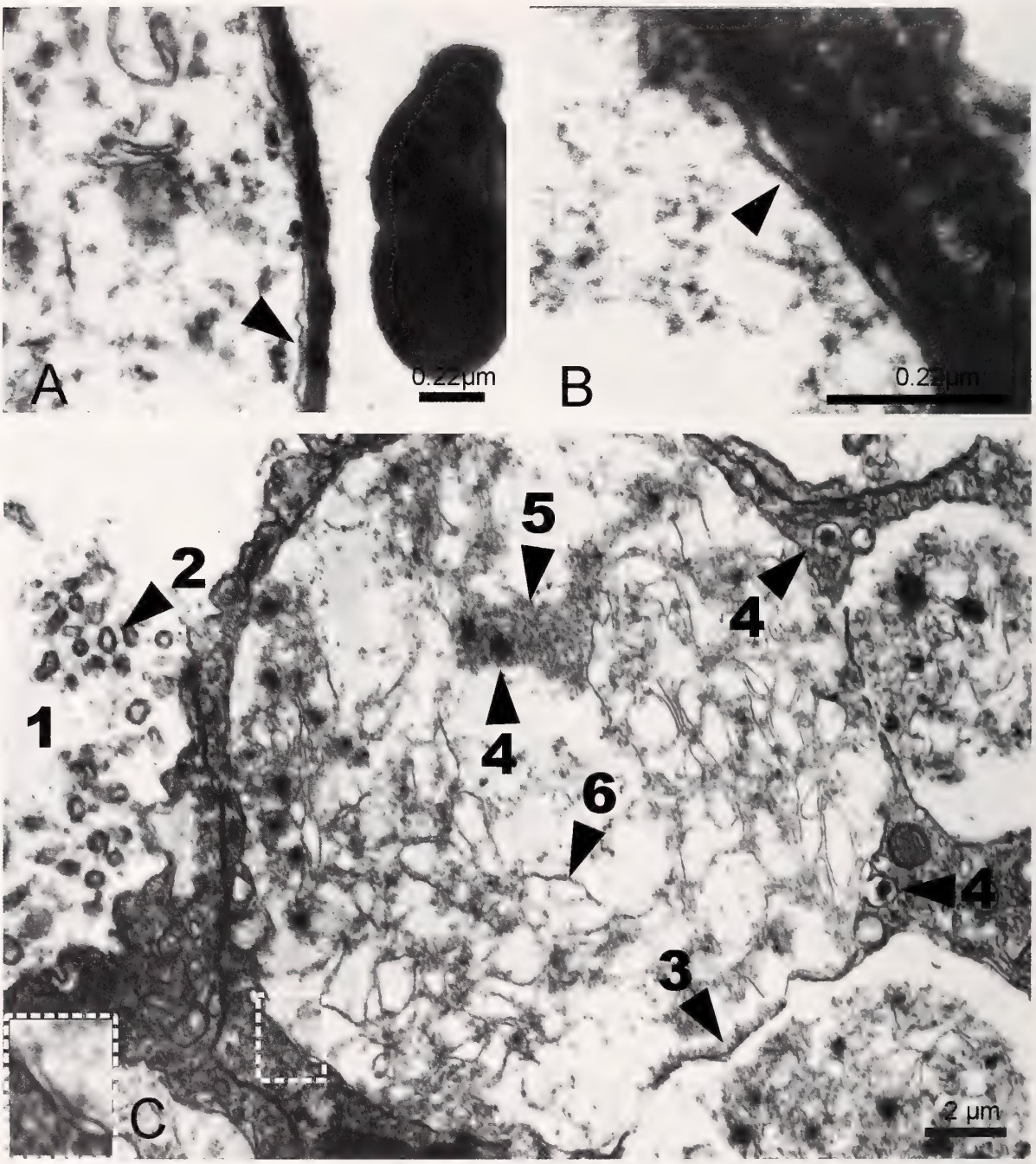


Figure 4. **A.** The wall of a fecal C corpuscle (scale bar = 0.2 µm) showing the outer membrane (◄) which is detached from it; the electron dense structures outside the C corpuscle are cocci. **B.** Outer membrane (◄) detached from the wall of a C corpuscle contained within a glandular cell (scale bar = 0.2 µm); the lipid bilayer can be recognized. **C.** A large body (scale bar = 2 µm), probably a nude C corpuscle that is located close to the alveolar lumen [1] where microvilli are seen [2]. Two similar smaller bodies appear as either fusing with the larger body, or alternatively, being split by new membrane formation [3]. Coarse granules [4] are seen in these bodies, both within buds protruding on the outer surface, and associated with numerous finer granules [5]. Also, an array of inner membranes is seen, particularly in the larger body [6]. The inset shows the double membrane lining this body (1.6 times the initial micrograph).

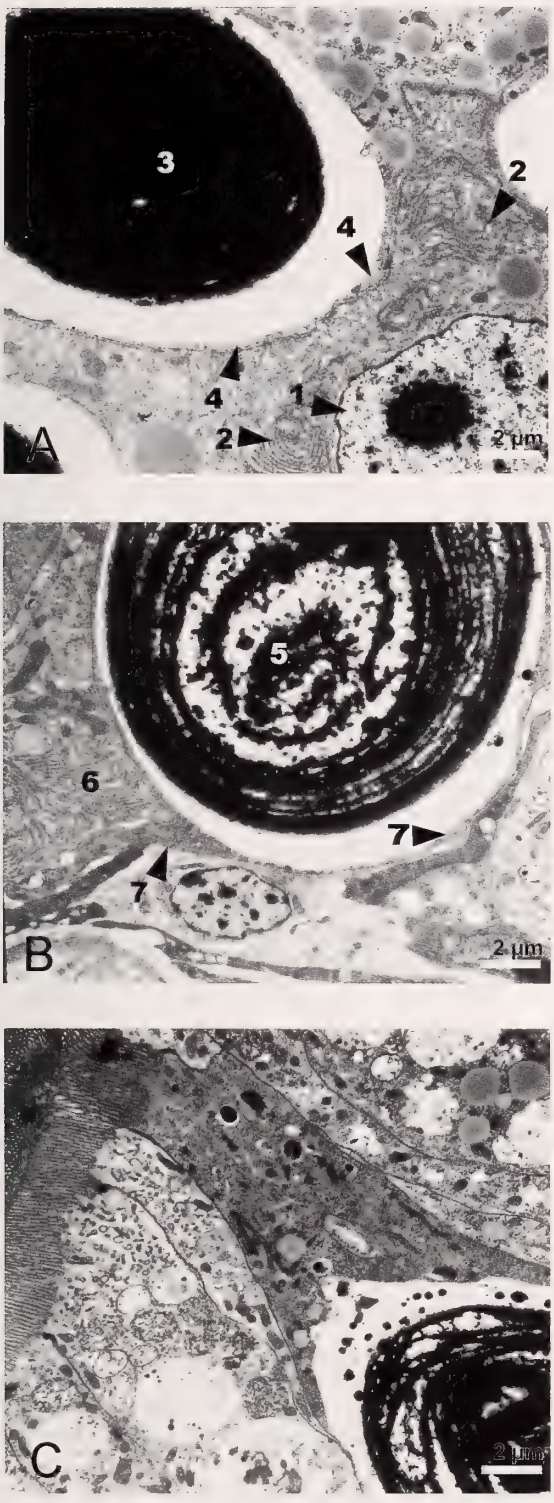


Figure 5. Electron micrographs (scale bars = 2 µm) of K corpuscles and associated structures. **A.** A large pyramidal cell nucleus [1] of a cell with a well developed rough endoplasmic reticulum (RER) [2]. The nearby K [3] corpuscle is surrounded, however, by a thin cytoplasmic band from a different cell [4]. **B.** A multilamellar K corpuscle [5] close to RER-bearing cytoplasm [6]; however, the corpuscle is also contained within a cytoplasmic band from another, more electron dense cell [7]. Clumps of high electron density material are contained within the same vesicle as the K corpuscle, and appear as being deposited on it. **C.** The lower micrograph shows the apex of a stereocilia-bearing cell containing a K corpuscle that is not surrounded by any cytoplasmic band. Clumps of an electron-dense material seem to be being absorbed in the stereocilia and appear to be being deposited on the K corpuscle.

to that of walled C corpuscles) are present, especially in the upper region of columnar cells (Figure 4). A double membrane can be recognized lining some of these bodies, which sometimes appear splitting. Budding structures containing a single large electron-dense granule can also be seen (Figure 4).

Pyramidal cells are less frequent than the columnar cells described above. They are large basophilic cells with a wide base and a large and basal nucleus (8.5 ± 0.5 µm in diameter) with a prominent nucleolus (Figure 2A). The nucleus is located close to the basal membrane. Dark corpuscles identical to fecal K corpuscles appear associated to these cells in light microscopy preparations. Each of them seems to be contained within the cytoplasm of pyramidal cells, usually with the wider base near the basal membrane and the narrower neck close to the lumen. The dimensions of such large structures are difficult to assess in tissue sections, where they appear sectioned in all possible spatial planes. We estimated length as the maximum diameter of those corpuscles in which the ratio between the maximum and minimum diameter was 1.5 or more, and width as the mean diameter of those corpuscles in which the maximum/minimum diameter ratio was less than 1.2. Under these conventions the length of K particles contained within pyramidal cells was 22.6 ± 1.2 µm and width was 15.0 ± 0.4 µm.

Electron microscopy of typical K corpuscles shows them contained within a large vesicle (Figure 5). This vesicle is usually lined by a narrow cytoplasmic band of varying electron density where mitochondria may be found. Particles of high electron density are deposited on the surface of the K corpuscle, coming from the cytoplasmic band surrounding it. The whole (i.e., the vesicle containing the K corpuscle and the narrow band of cytoplasm) is in turn surrounded by cytoplasm with a well developed rough endoplasmic reticulum (RER); when a nucleus is seen in the surrounding RER-bearing cytoplasm, it is always a large one (Figure 5). Since these large nuclei are likely to be those of pyramidal cells, K corpuscles would not actually be contained within pyramidal cells, but within the cytoplasm of a different cell (seemingly an extrusion of a columnar cell), which is in turn engulfed by a pyramidal cell.

Table 1

Pigmented areas in midgut glands of male and female *P. canaliculata.*

	C corpuscles* (%)	K corpuscles** (%)
Males	0.78 ± 0.18	5.15 ± 0.44
Females	1.92 ± 0.34	11.88 ± 2.28

* Pigmented areas that were in the chromatic range of C and K corpuscles and that were smaller than 30 μm^2, expressed as percent of the tissue section occupied by them; they correspond to the total area occupied by the darker areas of C corpuscles (i.e., a smaller area than the one occupied by whole C corpuscles). Significantly different by gender (Student's t test, $P < 0.01$).

** Pigmented areas that were in the chromatic range of C and K corpuscles and were larger than 30 μm^2, expressed as percent of the tissue section occupied by them; they correspond to the total area occupied by K corpuscles. Significantly different by gender (Student's t test, $P < 0.01$).

Sexual Differences in the Amount of Pigmented Corpuscles

Midgut glands of females in light microscopy preparations appeared to have a greater amount of pigmented material than those of males. Therefore the relative abundance of pigmented corpuscles in males and females was quantified in unstained preparations as the percent of the section surface occupied by pigmented areas. Although average pigment density is higher in K than in C corpuscles, the chromatic range was continuous between both types of corpuscles (i.e., dark areas of C corpuscles overlap with light areas in K corpuscles). Therefore, they were separated by estimating the total area occupied by dots smaller than 30 μm^2 (which correspond only to the pigment condensations within C corpuscles, and not to whole C corpuscles). Results are summarized in Table 1. The relative occupancy of the female midgut gland by C corpuscles (defined as explained above) and K corpuscles was approximately 2.4 times that in males (Student's t test, $P < 0.01$).

DISCUSSION

Pigmented "spherioles" in the midgut gland of gastropods have been recognized for more than a century. They have been regarded as containing "chlorophyllous pigments" derived from food, and/or as having an excretory function (see MacMunn, 1900, for early references). Meenakshi (1955) was probably the first to notice them in an ampullariid snail (*Pila virens* (Olivier, 1804)).

The present study of *Pomacea canaliculata* has shown some interesting and unexpected morphological features of both types of pigmented corpuscles that Andrews (1965) described in alveolar cells of the midgut gland of this species. As predicted by Andrews (1965) glandular C corpuscles are associated with alveolar columnar cells (which she calls "secretory and digestive cells"). They are granule-containing bodies surrounded by an electron dense wall, and are located within membrane vesicles of these cells. A membrane system composed of both irregular inner membranes and an outer lining membrane (located beneath the outer wall) could also be seen in some C corpuscles. No evidence of a nucleus was found in any case. Bodies similar to C corpuscles except that they were not lined by the outer wall, could also be seen contained within membrane vesicles, so that these corpuscles appeared lined by a double membrane. Since walled C corpuscles are not usually seen in the apical portion of columnar cells, and they are the only ones observed in the feces, the nude forms must either be digested after being released into the glandular lumen or acquire the wall during their passage through the gut.

Although K corpuscles appear contained within alveolar pyramidal cells ("excretory cells," Andrews, 1965) in light microscopic preparations, electron microscopy has shown they are actually contained within an extrusion of a cell with a small nucleus (i.e., a columnar cell) and that this extrusion is in turn engulfed by a pyramidal cell. K corpuscles occur more frequently than C corpuscles in glandular tissue, while C corpuscles are more frequent in the feces, which suggests that the rate of formation and elimination of K corpuscles may be very low.

C corpuscles that were essentially similar to glandular corpuscles were also observed in feces and in old aquarium sediments up to three years after sampling. A smaller number of K corpuscles is also eliminated in the feces by *P. canaliculata,* and they appear in aquarium sediments, but they tend to disappear with time.

The current results may be interpreted to mean that C corpuscles are not digestive enzyme carriers but the anuclear, thick-walled cells of a symbiont, which might also live outside the snail. K corpuscles may be interpreted as the cystic forms of that symbiont. The detection of significant amounts of DNA in both types of corpuscles (Castro-Vazquez et al., 2002) also favors this interpretation. This possibility should be tested with molecular biology techniques to determine the phylogenetic affinities of corpuscular DNA.

Another possible interpretation is that C corpuscles might be large residual bodies of intracellular digestion. The great variability we have observed in the content of C corpuscles might favor this hypothesis. However, the significance of K corpuscles, which seem to be derivatives of C corpuscles, as well as the presence of DNA in both types of corpuscles would be left unexplained by a residual bodies hypothesis.

We have not yet any testable hypothesis for explaining the larger amount of pigmented material present in the midgut glands of female snails, than in those of male snails. If both C and K corpuscles finally prove to be morphs of a symbiont, some nutritional advantage related to the requirements of the high reproductive investment

of female *P. canaliculata* (Albrecht et al., 1999, 2004) will have to be explored.

Acknowledgments. This work was supported by grants from CONICET, ANPCyT, and the National University of Cuyo. The generous help of Professor Beatriz C. Winik (National University of Tucuman, Argentina) and the criticisms of Professor Luis S. Mayorga (National University of Cuyo, Argentina) are gratefully acknowledged.

LITERATURE CITED

Albrecht, E. A., N. B. Carreño & A. Castro-Vazquez. 1999. Quantitative study of environmental factors influencing the seasonal onset of reproductive behavior in the South American apple-snail *Pomacea canaliculata* (Prosobranchia: Ampullariidae). Journal of Molluscan Studies 65:241–250.

Albrecht, E. A., E. Koch, N. B. Carreño & A. Castro-Vazquez. 2004. Control of the seasonal arrest of copulation and spawning in the applesnail *Pomacea canaliculata* (Prosobranchia: Ampullariidae): differential effects of food availability, water temperature, and day length. The Veliger 47: 147–152.

Andrews, E. B. 1965. The functional anatomy of the gut of the prosobranch *Pomacea canaliculata* and some other pilids. Proceedings of the Zoological Society of London 145:19–36.

Castro-Vazquez, A., E. A. Albrecht, I. A. Vega, E. Koch & C. Gamarra-Luques. 2002. Pigmented corpuscles in the midgut gland of *Pomacea canaliculata* and other neotropical apple-snails (Prosobranchia, Ampullariidae): a possible symbiotic association. Biocell 26:101–109.

Clark, G. 1981. Staining Procedures. 4th ed. Williams & Wilkins: Baltimore, MD.

MacMunn, C. A. 1900. On the gastric gland of Mollusca and Decapod Crustacea: its structure and functions. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 193:1–38.

Meenakshi, V. R. 1955. The excretory spherioles in the digestive gland of *Pila virens*. Journal of Animal Morphology & Physiology 3:75–78.

The Veliger 48(1):26–45 (June 30, 2006)

THE VELIGER

Diversity and Abundance of Tropical American Scallops (Bivalvia: Pectinidae) from Opposite Sides of the Central American Isthmus

J. TRAVIS SMITH[1], JEREMY B. C. JACKSON[1,2], AND HELENA FORTUNATO[2]

[1]Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093-0244, USA
[2]Center for Tropical Paleoecology and Archeology, Smithsonian Tropical Research Institute, Box 2072, Balboa, Republic of Panama

Abstract. There is confusion about the comparative diversity of mollusks on opposite sides of the Isthmus of Panama due to inadequate sampling and contrasting patterns of diversity for different molluscan taxa. We report here on the occurrence of scallops (Bivalvia: Pectinidae) from extensive new dredge sample collections from the Gulf of Panama and Gulf of Chiriqui in the Eastern Pacific and from the San Blas archipelago to the Cochinos Cays in the Gulf of Honduras in the southwestern Caribbean. The collections contain more than 8000 specimens of 33 species from 213 collections. These include 22 Caribbean species and 11 Eastern Pacific species. However, the average abundance of scallops per collection is much higher in the Eastern Pacific so that the average number of species per collection was similar in the two oceans. This discrepancy in abundance is the principal reason previous workers have erroneously concluded that species diversity is equal or even greater in the Eastern Pacific than the Caribbean. Numbers of scallop species at the seven different Caribbean localities sampled average about one and one half times higher than the two regions in the Eastern Pacific, and the total differences in species richness are two times higher for all the regions combined. Most scallop species were common to abundant and scallop species do not exhibit a log series or log normal pattern of relative abundance. However, we found eight previously undescribed species, two in the Eastern Pacific and six in the Caribbean. These appear to be geminate species and are indistinguishable, pending detailed morphological study, from species occurring in the opposite ocean. These new species are all rare but typically occurred in sufficient abundance and at numerous localities so that their occurrence is not in question.

INTRODUCTION

The rise of the lower Central American Isthmus divided the once continuous tropical American ocean into two very different realms (Birkeland, 1977, 1987; Coates et al., 1996; D'Croz and Robertson, 1997; Jackson & D'Croz, 1998). Formation of the Isthmus occurred over about 20 million years (Coates et al., 2003) and the final separation of the oceans around 3.5 to 3.0 million years ago (Coates & Obando, 1996). Coastal environments on the two sides of the Isthmus are very different (Birkeland, 1977, 1987; Jackson & D'Croz, 1998). The tropical Eastern Pacific exhibits strong seasonal and inter-annual fluctuations in temperature and primary production associated with upwelling and El Niño events. Primary productivity of phytoplankton is great but coral reefs are poorly developed and seagrasses absent. In contrast, the tropical Western Atlantic exhibits much smaller seasonal and inter-annual variability, low planktonic productivity, and extensive development of coral reefs and seagrass meadows.

The isolation of the oceans also resulted in widely diverging patterns of evolution and taxonomic diversity among major taxa that were formerly quite similar across the developing Isthmus (Vermeij, 1978, 1993; Lessios, 1990; Jackson et al., 1993, 1996; Knowlton et al., 1993; Knowlton and Weight, 1998; Budd, 2000). Numbers of species of reef corals (Veron, 2000), cheilostome bryozoans (Cheetham & Jackson, 2000), and benthic foraminifera (Buzas & Culver, 1991; Collins, 1999) are considerably greater in the Western Atlantic than the Eastern Pacific, whereas crustaceans (Jones & Hasson, 1985) and echinoderms (Chesher, 1972) differ little across the Isthmus.

The diversity patterns for mollusks have been the subject of much confusion and debate because of great differences in sampling effort and taxonomic study. Woodring (1966) and subsequently others (Stanley & Campbell, 1981; Vermeij & Petuch, 1986; Petuch, 1995) concluded that the Western Atlantic fauna had suffered high extinction during the Pliocene that reduced diversity compared to the Eastern Pacific. However, more recent studies demonstrate that high extinction was balanced by high origination (Allmon et al., 1993, 1996; Jackson et al., 1993, 1999) and that the numbers of species in the two oceans are approximately the same (Roy et al., 2000).

In contrast, the diversity patterns of lower taxonomic levels exhibit great variation across the Isthmus. For example, gastropods of the *Strombina* Group have much higher diversity in the Eastern Pacific than the Western

Table 1

Previous studies covering the Caribbean, Gulf of Mexico, and Eastern Pacific regions.

Pacific studies	Taxa
Grau, 1959	9
Olsson, 1961	9
Keen, 1971	9
Previously described species	9
This study	11
Caribbean studies	**Taxa**
Olsson and McGinty, 1958	5
Abott, 1958	7
Bayer et al., 1970	15
Waller, 1973	18
Vokes and Vokes, 1983	12
Rios, 1985	10
Cahill, 1990	15
Merlano and Hegedus, 1994	16
Abbott and Morris, 1995	13
Mikkelsen and Bieler, 2000	22
Redfern, 2001	11
Previously described species	25
This study	25

Atlantic (Jung, 1989; Jackson et al., 1993, 1996; Fortunato, 1998). Similarly, the bivalve genus *Chione* is approximately twice as diverse in the eastern Pacific (Roopnarine, 2001). In contrast, the scallops in the Family Pectinidae are more diverse in the Western Atlantic (Table 1).

Mollusks of the tropical Eastern Pacific have been sampled more extensively than tropical Western Atlantic mollusks. There are no major compendia of the tropical Western Atlantic fauna comparable to those for the tropical Eastern Pacific (e.g., Grau, 1959; Olson, 1961; Keen, 1971; Coan et al., 2000); although numerous studies document the faunas of more limited areas such as the Bahamas (Redfern, 2001), Bermuda (Waller, 1973), Brazil (Rios, 1985), Colombia (Merlano & Hegedus, 1994), Florida Keys (Mikkelsen & Bieler, 2000), Jamaica (Humfrey, 1975), Panama (Olsson & McGinty, 1958; Radwin, 1969; Bayer et al., 1970), Cuba (Espinosa et al., 1994), and the Yucatan Peninsula (Ekdale, 1974; Vokes & Vokes, 1983).

Recent tropical Eastern Pacific scallops have been described in three monographs (Grau, 1959; Keen, 1971; Olsson, 1961) each of which described all nine known species. In contrast, the Family as a whole has not been fully documented in any one study for the Western Atlantic although different genera have been described in detail including *Argopecten* (Waller, 1969), *Nodipecten* (Smith, 1991), and the "chlamid" genera *Caribachlamys, Laevichlamys,* and *Spathochlamys* (Waller, 1993). Twenty-five species of scallops have been described from the tropical Western Atlantic but no one published report includes all the species and the average number of species per paper is 13. The highest reported diversity in one region is 22 from the Florida Keys (Mikkelsen & Bieler, 2000), and this was a compilation based on museum collections, private collections, and publications.

Here we describe the diversity and abundance of scallops from opposite sides of the Central American Isthmus obtained by extensive dredging along the Pacific coast of Panama and the Caribbean coast of Panama, Nicaragua, and Honduras. The very large numbers of samples and specimens allowed us to evaluate possible effects of sampling bias and to describe patterns of species diversity and relative abundance with confidence.

MATERIALS AND METHODS

All samples were obtained by Helena Fortunato from 1995 to 1998 as part of the Panama Paleontology Project using a bottom dredge and the research vessel *RV Urraca* of the Smithsonian Tropical Research Institute. The dredges were built at STRI and ranged in size from 27 to 29 inches in width, 17 to 27 inches in height, trailing a net with 1 inch mesh. The dredges were towed for 5 to 20 minutes depending on bottom conditions and depth and were usually brought up clogged and full of sediment. The 79 samples from the Eastern Pacific were obtained from depths of 6 to 380 meters depth and the 150 Caribbean samples from 7 to 538 meters. However, most of the samples from both oceans were from less than 100 meters depth. The geographic locations of all the samples are shown in Figure 1 and the details of locations, depth, and bottom characteristics for all the samples can be found at the PPP website (http://www.fiu.edu/~collinsl/index.html).

The samples were washed and sieved on deck using 8 mm and 2 mm mesh. Samples were sorted at STRI and all bivalves identified to genus or subgenus before shipment to the Scripps Institution of Oceanography. All scallops were identified to species by the first author.

Additional material examined for taxonomic reference included scallops from the Gibson-Smith collections of Venezuelan mollusks now housed at the Naturhistorisches Museum in Basel Switzerland (NMB), and from the first author's collections from deposits in the Enriquillo Valley in southwestern Dominican Republic and Bocas del Toro, Panama. Material from these additional collections was not used in analyses of diversity and abundance.

Diversity was measured as the number of species (richness), the Shannon-Weiner index of diversity H, calculated as $H = -\Sigma\ p_i \log\ p_i$, and Fisher's Alpha ($\alpha$) as $N/S = (e^{S/\alpha} - 1)/(S/\alpha)$. The latter is a best-fit solution for α. Both metrics were calculated using the STATPOD package for the statistics software R (Johnson & McCormick, 1999).

TAXONOMY AND SYSTEMATICS

Our goal was to describe patterns of species occurrences and abundance across the Isthmus without attempting

Figure 1. Locality maps. Central map shows the geographic locations of the localities used in this study. Surrounding maps show regional localities for (A) Cochinos Cays, Honduras, (B) Mosquito Cays, Nicaragua, (C) Bocas del Toro, Panama, (D) San Blas, Panama, (E) Gulf of Chiriqui, Panama, and (F) Gulf of Panama, Panama. Small letters on the Bocas del Toro map (C) depict the regions used in the study. These are (a) Almirante Bay, (b) Chiriqui Lagoon, (c) Bocas del Toro, and (d) Gulf of Mosquitoes.

any systematic revision of higher taxonomic categories that would be inappropriate without thorough examination of material from outside the region of study. In general, we followed the systematic framework of Waller (1969, 1986, 1991, 1993) that has received strong support from independent molecular genetic data based on mitochondrial cytochrome c oxidase CO1 (Matsumoto & Hayami, 2000) and mitochondrial 16s and 12S rRNA genes (Barucca et al., 2004). Additional sources for taxa not covered in Waller's work include Grau (1959), Olsson (1961), Keen (1971), Moore (1984), Rios (1985), Smith (1991), Abbott and Morris (1995), and Coan et al. (2000).

We did not subdivide genera into subgenera because of inconsistent usage in the literature, and because species within the different genera could be consistently and un-

ambiguously distinguished on the basis of one or more characters regardless of their subgeneric classification. The only exception is *Pseudamussium* (*Peplum*) as traditionally used for the species *P.* (*P.*) *fasciculatum* (Hinds, 1845) (Figures 2I, J, M, N). *Nodipecten* has been considered both a subgenus of *Lyropecten* (Keen, 1971; Jackson et al., 1999) and as a separate genus (Smith, 1991; Abbott & Morris, 1995; Coan et al., 2000). *Nodipecten* can be separated from species of *Lyropecten* based on the ribbing pattern (Smith, 1991). Members of the genus *Lyropecten* have a left valve ribbing pattern of r-RrrRcrrRr or rNrrNcrrNr where r represents a rib, R a key or more pronounced rib, N represents a key rib with nodes, and Nc signifies the central, noded rib following Smith (1991). In *Nodipecten* this arrangement is rRr-RcrRr or rNrNcrNr. The species *Nodipecten arthriticus* (Reeve, 1853) (Figures 3D, E) and *Nodipecten* sp. G (Figure 3C) are problematic in that they have the ribbing pattern rNrrNcrNr, which is intermediate to the characteristics of *Lyropecten* and *Nodipecten.* However, pending systematic revision, we have placed species with this ribbing pattern in the genus *Nodipecten* following Smith (1991) and Coan et al. (2000).

Pacipecten has been considered as a subgenus of both *Leptopecten* (Keen, 1971) and *Aequipecten* (Olsson 1961), and as a separate genus (Moore, 1984). Olsson (1961) originally described *Pacipecten* as a subgenus of *Aequipecten.* Later workers have gone back and forth treating the group as a subgenus or a genus. Species of *Pacipecten* and *Leptopecten* appear to form a clade and can be consistently separated from other groups based on their hinge morphology. In both genera there are two pairs of hinge teeth on the right valve and the anterior resilial tooth is the dominant tooth (Figure 4A). The genus *Pacipecten* can be separated from *Leptopecten* by the very fine or absent concentric lirae, making the shell appear almost smooth, and the absence of secondary or tertiary ribbing (Figure 5C). In the genus *Leptopecten* the concentric lirae are strong, often creating a flange-like appearance, and secondary or tertiary ribs are present in all of the tropical American species, although not in a consistent manner (Figure 5A, B).

The genus *Euvola* is the most problematic. Waller (1991) combined the living tropical American species previously assigned to the genera *Oppenheimopecten, Flabellipecten,* and *Amusium* into the genus *Euvola* based on observations that the species in question share certain morphological traits, and are quite certainly not members of the genera to which they have traditionally been assigned. While there are morphologic characters that apparently separate the species herein assigned to this genus into identifiable groups, the systematic approach of Waller has been followed here pending further work.

We used open nomenclature for the species Pectinid A *lineolaris* (Lamarck, 1819) (Figure 6A, B). This species has most recently been assigned to the genus *Argopecten* (Waller, 1969, 1991). The morphology of the hinge teeth indicates a close relationship with this genus. However, the early dissoconch microstructure of the left valve is unique to this species among those observed in these collections. In members of the genus *Argopecten,* as in all of those genera in the "*Aequipecten*" group observed in this study—*Lindapecten, Pacipecten,* and *Leptopecten*—a microstructure consisting of coarse pitting begins very early in the early dissoconch stage (Figure 7A, B). In Pectinid A the onset of this structure is delayed or extremely reduced (Figure 7C, D). In this case, as in the genera discussed above, the generic placement is not crucial to the analyses presented here. The diversity and rarity data presented are all based on species level identifications and are not examined at the genus level.

Species were identified using easily observed morphologic characters. Examples of all species identified and used in the analyses presented here are illustrated in Figures 2, 3, 6, 9–13. These figures also include several specimens that were used for comparison with observed species. The most readily observed character is valve symmetry. Species traditionally placed in the subfamily Pectininae have highly asymmetrical valves. The left (upper) valve is generally flat or even concave and the right (lower) valve is convex (Figure 8C, D). In all other species in the family, the valves are equal to sub-equal in convexity (Figure 8A, B). However, recent molecular work has questioned of the validity of this character for defining sub-familial groups within the Pectinidae (Frischer et al., 1998; Canapa et al., 2000; Steiner & Muller, 1996; Barucca et al., 2003). This apparent disconnect between traditional, easily observed morphologic characters and phylogenetic relationships based on molecular data is the primary reason for our decision to analyze diversity only at the species level pending further systematic work on the group to sort out higher level taxonomic relationships.

Hinge teeth are also an important taxonomic character as discussed above in regards to *Pacipecten* and *Leptopecten.* Waller (1986, 1991) presented a consistent identification and nomenclatural scheme for pecten hinge teeth, also called crura. The primary morphologic differences in hinge teeth relate to number of pairs and dominance of the teeth, illustrated in Figure 4, which differs depending on the left and right valves of the taxon in question. The remaining characters used for identification of species are rib count, presence or absence of secondary or tertiary ribbing, presence and strength of concentric lirae, and pattern of rib dominance and ribs with nodes.

In this study we have identified several taxa that are heretofore undescribed and are designated informally as species A, B, etc. In all but two cases these taxa are similar to species known from the opposite ocean and

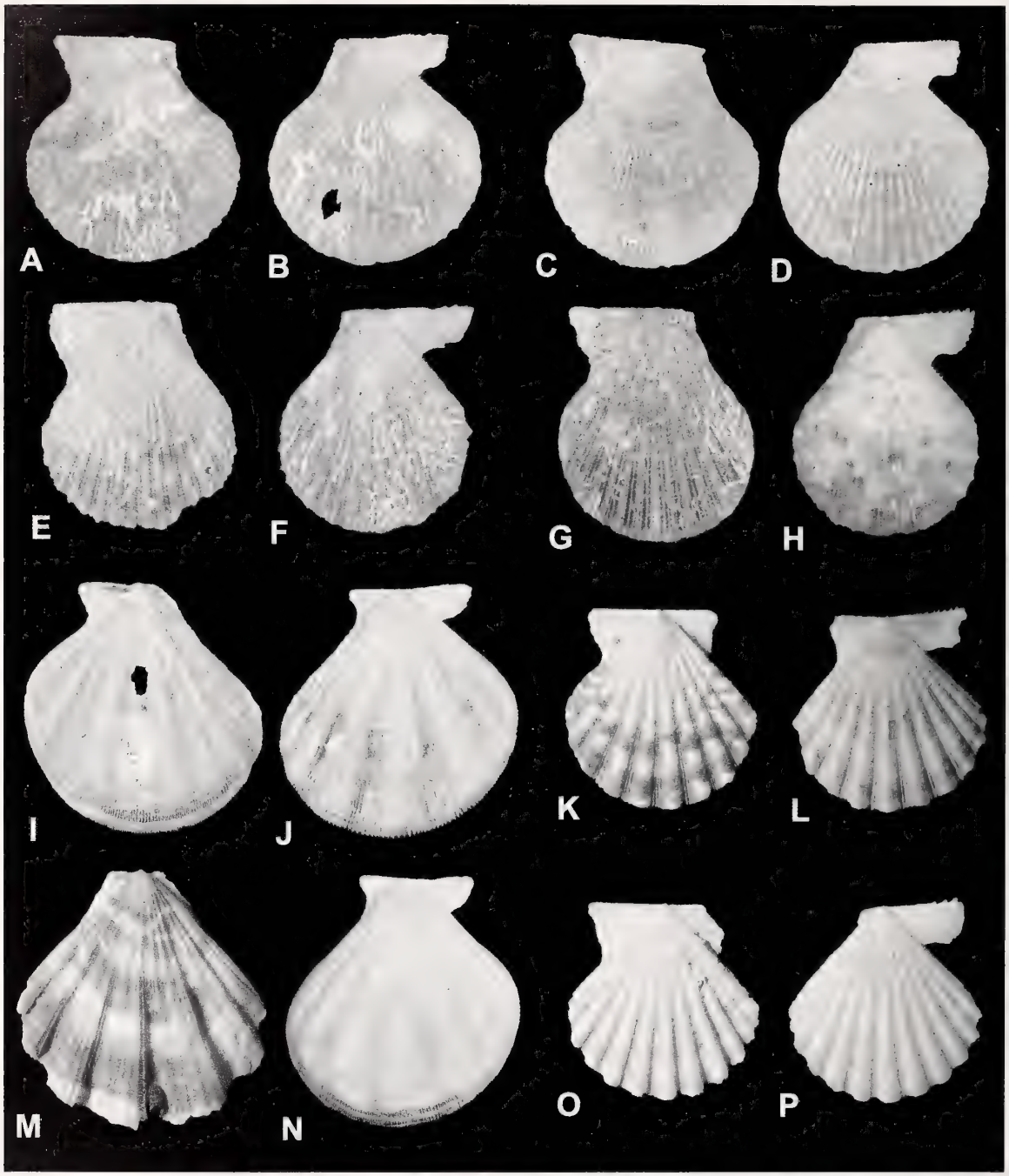


Figure 2. *Spathochlamys, Pseudamussium* (*Peplum*), and *Bractechlamys.* (A) *Spathochlamys benedicti* (CTPA 540-B-52, lvh = 14.15 mm), (B) *S. benedicti* (CTPA 493-B-124, rvh = 15.79 mm), (C, D) *S. cf. vaginula* (jts 06-B-11, (C) lvh = 16.27 mm, (D) rvh = 13.13 mm), (E, F) *S. vestalis* (CTPA 399-B-146, (E) lvh = 12.36 mm, (F) rvh = 13.13 mm), (G, H) *S.* sp. A (CTPA 538-B-101, (G) lvh = 14.79 mm, (H) rvh = 14.08 mm), (I, J) *Pseudamussium* (*Peplum*) *fasciculatum* (CTPA 415-B-72, (I) lvh = 29.81 mm, (J) rvh = 28.15 mm), (K, L) *Bractechlamys antillarum* (CTPA 431-B-72, (K) lvh = 16.35 mm, (L) rvh = 18.55 mm), (M) *P.* (*P.*) sp. D (CTPA 525-B69, lvh = 18.87 mm), (N) *P.* (*P.*) sp. D (CTPA 338-B-85, rvh = 28.0 mm), (O) *B.* sp. H (CTPA 362-B-1, lvh = 14.09 mm), (P) *B.* sp. H (CTPA 412-B-1, rvh = 14.04 mm).

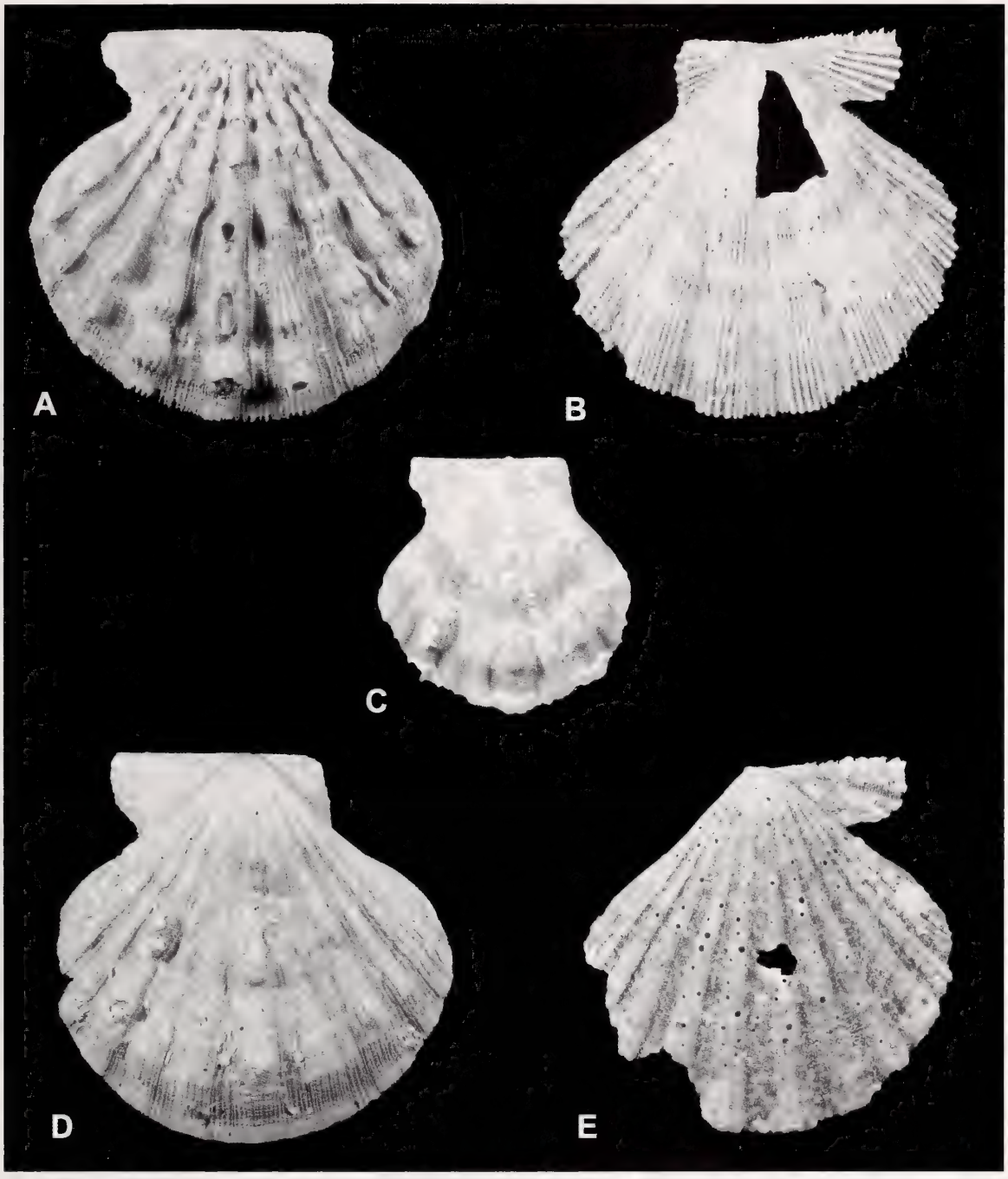


Figure 3. *Nodpipecten.* (A) *Nodipecten nodosus* (jts 06.13-B-13, lvh = 85.75 mm), (B) *N. nodosus* (CTPA 403-B-84, rvh = 66.81 mm), (C) *N.* sp. G. (CTPA 494-B-57, lvh = 15.36 mm), (D) *N. arthriticus* (CTPA 403-B-45, lvh = 97.37 mm), (E) *N. arthriticus* (CTPA 389-B-84, rvh = 53.05 mm).

may be geminate species pairs. The two undescribed species that are not considered geminate species are *Euvola* sp. cf. *E. raveneli* (Dall, 1898) (Figure 9F), which is represented by very few identifiable specimens, and *Caribachlamys* sp. cf. *C. mildredae* (Bayer, 1941) (Figure 10A, B). The latter species was found by the first author while snorkeling in Bocas del Toro but not in any of the dredge samples, and is therefore not included in the analyses of diversity. A final species, tentatively identified as *Euvola* cf. *laurenti* (Gmelin, 1791), was not included in

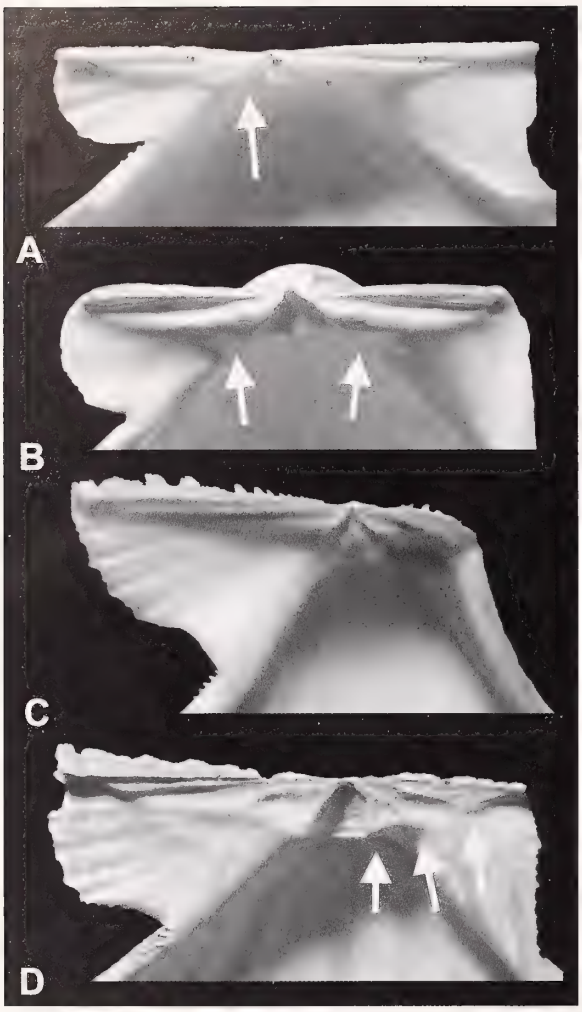


Figure 4. Illustration of the described hinge morphologies. Two pairs of hinge teeth with the anterior resilial tooth dominant (A). Two pairs of hinge teeth with the resilial teeth dominant and extended (B). Two pairs of hinge teeth with no dominant teeth (C). More than two pairs (3 in this case) of hinge teeth (D). Specimens shown are (A) *Pacipecten tumbezensis* (CTPA 381-B-70, hl = 25.54 mm), (B) *Argopecten gibbus* (NMB 17662, hl = 31.52), (C) *Caribachlamys* cf. *mildredae* (jts 11-B-1, hl = 14.32), and (D) *Nodipecten nodosus* (NMB G 17477, hl = 64.34). Terminology follows Waller (1986, 1991, 1993).

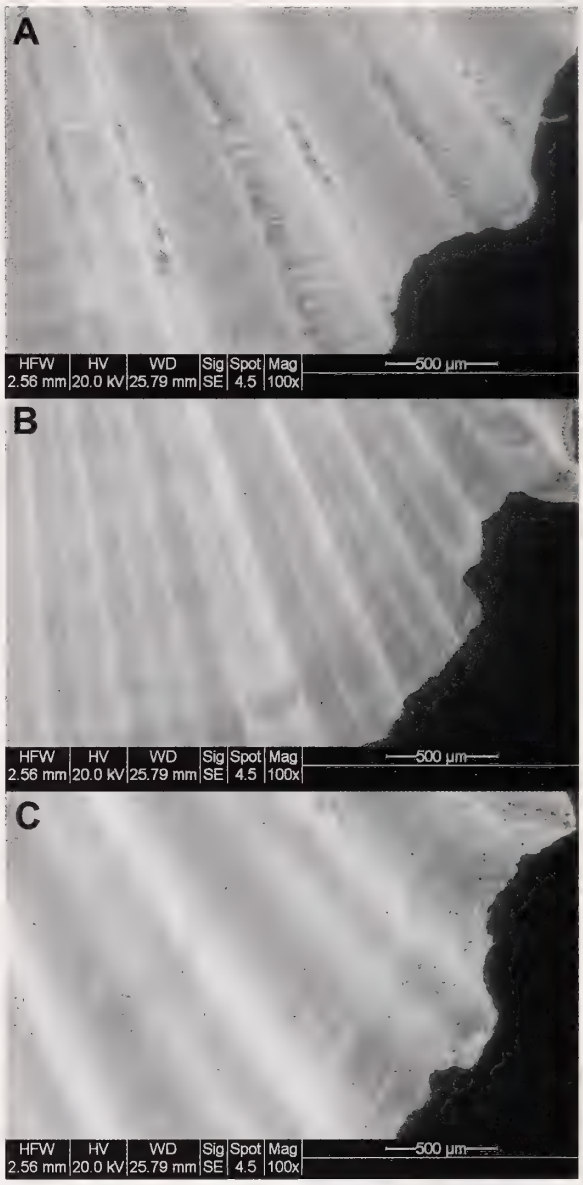


Figure 5. Shell morphology of *Leptopecten* and *Pacipecten*. The characteristics of *Leptopecten* (A, B) are strong concentric lamellae and the presence, in most taxa, of secondary ribbing, and in *Pacipecten* (C) are very fine concentric lamellae and absence of secondary or tertiary ribbing. Specimens shown are (A) *Leptopecten biolleyi* (CTPA 387-B-151), (B) *Leptopecten bavayi* (CTPA 577-B-34), and (C) *Pacipecten linki* (CTPA 458-B-100).

this study because it occurred as a single fragment from one sample in the Eastern Pacific.

PATTERNS OF SPECIES DIVERSITY

We obtained 3915 specimens of 11 species of scallops in 74 samples from the Eastern Pacific and 4434 specimens of 22 species in 139 samples from the Caribbean (Table 2). The number of living specimens was less than 0.1% of the total, so these results are based on time-averaged assemblages representing hundreds to thousands of years (Kidwell, 2002a). Death assemblages have been shown to faithfully represent the relative abundance of the local fauna (Kidwell, 2001, 2002a). This is particularly true when the focus is on larger mesh sizes (> 1.5 mm) as is the case in this study (Kidwell, 2002b). Collector's curves of numbers of species found as a function of numbers of specimens or samples level off well before all the samples are included so that the differences in diversity are robust (Figure 14). However, the abundance of specimens per

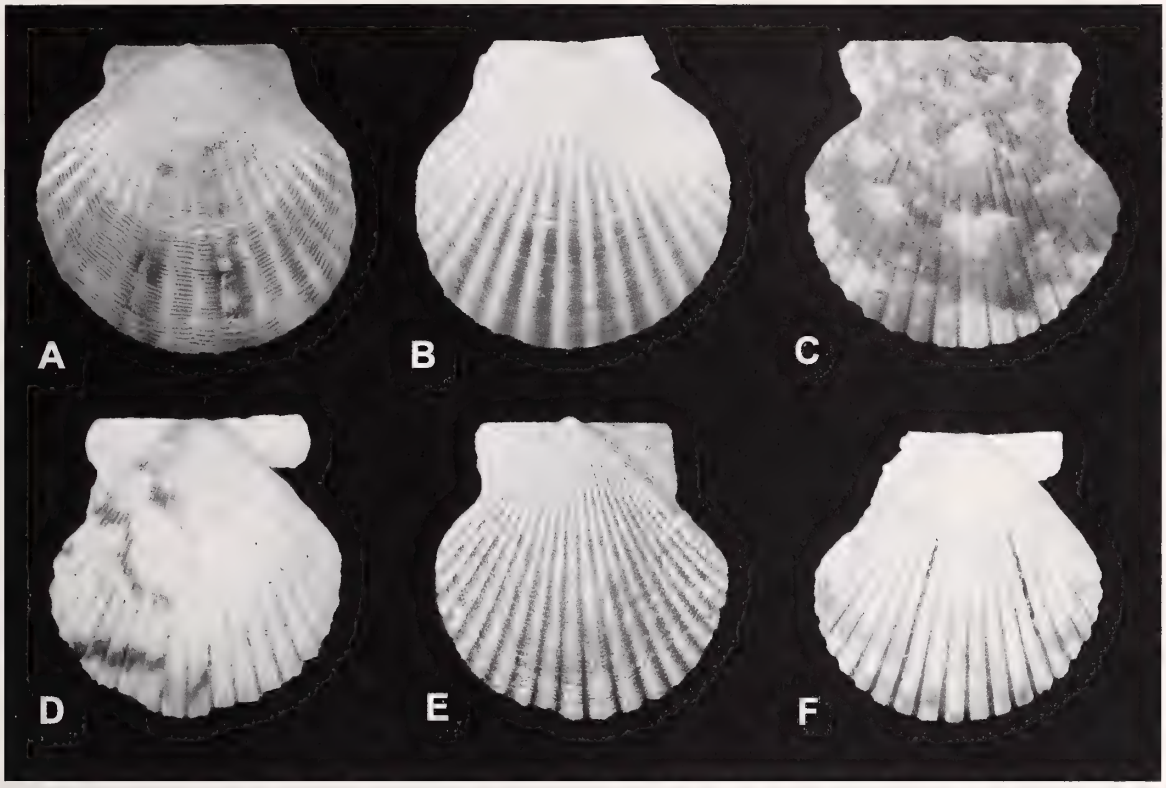


Figure 6. *Argopecten* and Pectinid A. (A, B) PectinidA *lineolaris* (NMB G 17478, both valves height = 39.69 mm), (C) *Argopecten gibbus* (CTPA 326-B-25, lvh = 19.57 mm), (D) *A. gibbus* (CTPA 336-B-47, rvh = 15.72 mm), (E, F) *A. ventricosus* (CTPA 399-B-27, (E) lvh = 16.70 mm, (F) rvh = 13.02 mm).

dredge sample was much greater in the Pacific collections (2×2 contingency table, chi square = 556.72, $P \ll 0.0001$). Nearly twice the number of samples in the Caribbean yielded only 12% more specimens than were collected in the Pacific. There are two important consequences of these differences in abundance between the oceans. First, the average number of species per locality is about four in both oceans, despite the much greater overall diversity in the Caribbean (Figure 15A). Second, the sampling curves are slightly flatter for the Eastern Pacific collections. More specimens per locality equate to higher local species richness and more complete sampling with lower effort.

In the Eastern Pacific, numbers of species were lower in the Gulf of Panama than the Gulf of Chiriqui (Table 3). There were only small differences in the Shannon-Weiner Index (H) and Fisher's Alpha (α) diversity measures between these two regions. Diversity in the Gulf of Chiriqui was slightly lower using H and slightly higher using α. We found all nine of the previously described species from the Eastern Pacific, although not always in both regions. The two additional species reported here are undescribed and are apparently geminate species (Table 4). *Lindapecten* sp. B (Figure 11C, D) was found in both the Gulf of Panama and Gulf of Chiriqui, but *Bractechlamys* sp. H (Figure 2O, P), was found only in the Gulf of Chiriqui. *Lindapecten* sp. B is virtually indistinguishable from *L. acanthodes* (Dall, 1925) (11A, B) in the Caribbean as is *Bractechlamys* sp. H from *B. antillarum* (Recluz, 1853) (Figure 2K, L) in the Caribbean. Both species were identified from well-preserved complete specimens collected at multiple localities (Table 2).

Sampling completeness was not as good in the Caribbean as in the Eastern Pacific. All of the Caribbean regions except Bocas del Toro contained only two thirds or less of the total Caribbean species collected. Species richness ranged from 14 to 17 species for all the regions except Bocas del Toro (Table 3), and sampling curves were indistinguishable except for the latter region. The Shannon-Weiner Index (H) is highest ($H > 1.9$) in the Bocas del Toro, San Blas, Almirante Bay, and Cochinos Cays regions. H was lowest ($H < 1.8$) in the Mosquito Cays, Gulf of Mosquitoes, and Chiriqui Lagoon regions. There is very little difference among these groups. Fisher's Alpha (α) was highest ($\alpha > 3.6$) in the Bocas del Toro, Gulf of Mosquitoes, and Los Cochinos regions. Alpha was lowest ($\alpha < 3.1$) in the Chiriqui Lagoon, Mosquito Cays, and Almirante Bay regions. The San Blas region was intermediate between these groupings.

We found 6 new species in the Caribbean samples, all

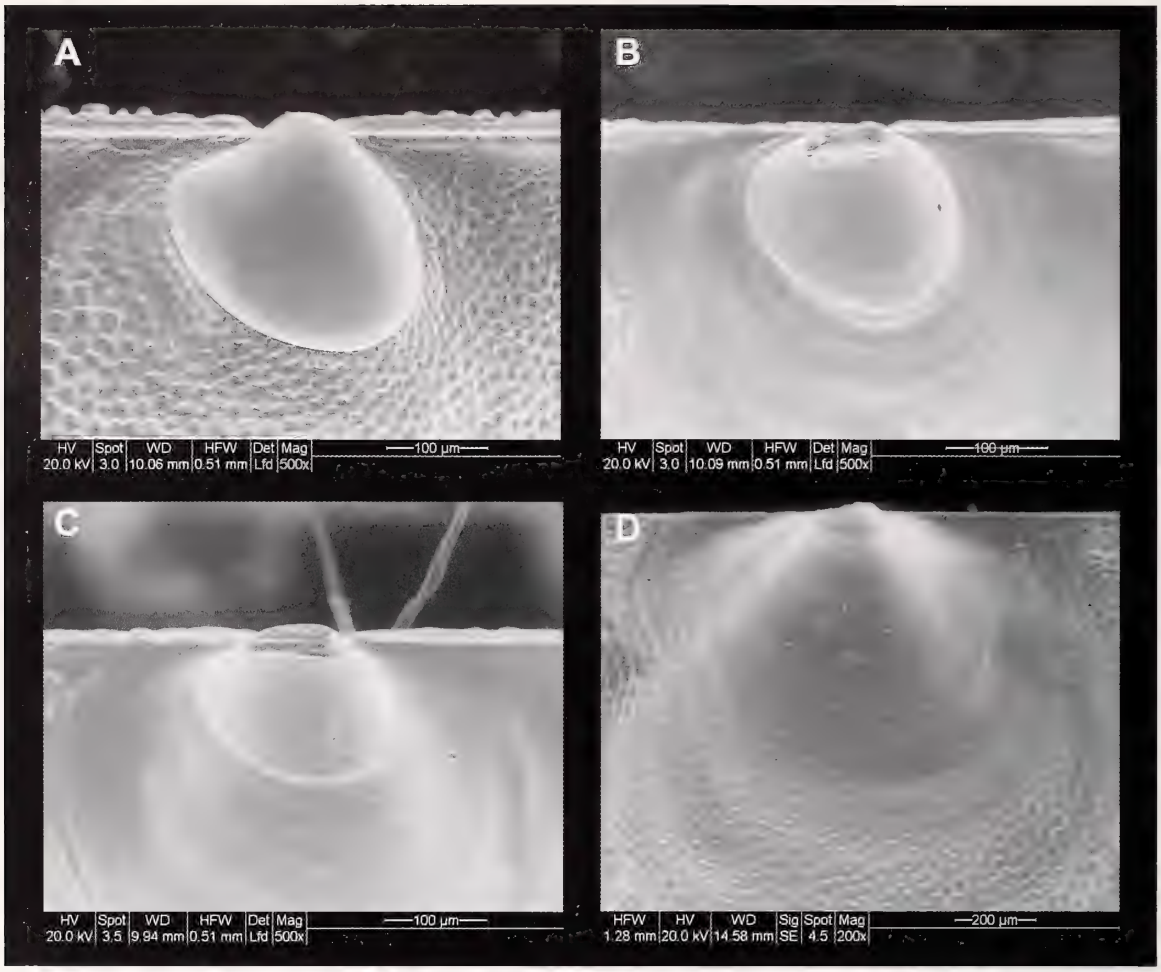


Figure 7. Left valve early dissoconch microstructure. *Aequipecten* like structure (A, B) showing early origination of pitted microsculpture and (C, D) the modified form seen on specimens assigned herein to the genus Pectinid A showing delayed onset of pitted microsculpture. Specimens shown are (A) *Leptopecten biolleyi* (CTPA 373-B-89), (B) *Argopecten gibbus* (CTPA 482-B-15) and (C and D) Pectinid A *lineolaris* (CTPA 519-B-106-1 and 519-B-106-2).

of which were rare. All of these undescribed species appear to be geminate sister species to taxa in the Eastern Pacific (Table 4) and are so far indistinguishable morphologically based on the small numbers of specimens available. An additional species, represented by 15 left valves, may be *Euvola raveneli* but due to the lack of right valve specimens we are considering it *Euvola* sp. cf. E. raveneli. No specimens of *E. raveneli* were positively identified in the collections.

COMMONNESS AND RARITY

The tropical American scallops do not fit a typical log series or log normal pattern of relative abundance (Figure 15A) observed for mollusks as a whole (Buzas et al., 1982), but more closely resemble abundance patterns of free-living bryozoans from the same region (Cheetham & Jackson, 2000). Most of the species are common to abundant and there are fewer rare species compared to other groups. Five out of the 11 Eastern Pacific species (45%) were found in more than 20% of the samples whereas only 7 of the 21 Caribbean species (33%) occurred as frequently (Figure 15B). Despite the poor statistical fit to a log normal distribution, we can perform the exercise of estimating the effect additional sampling would have for discovering additional species in the two oceans (Buzas et al., 1982). In the eastern Pacific a doubling of sampling effort would be assumed to produce roughly 1 or 2 more species. In the Caribbean this number is a little higher, between 2 and 3. In fact, we know that our collections do not contain 5 species of scallop that are described from the Caribbean and the Gulf of Mexico.

Rabinowitz (1981) defined rarity in terms of geographic range and abundance (see also Gaston, 1994). We plotted the proportion of localities in which the species occurs

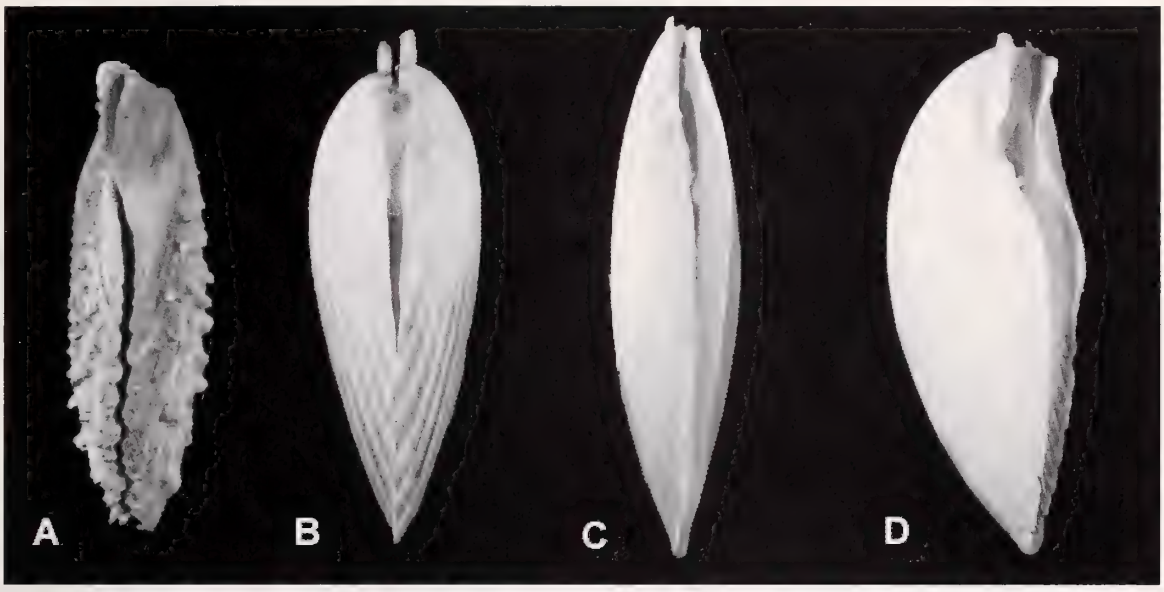


Figure 8. Shell symmetry. Illustration of the common forms of shell convexity in scallops. Equal to sub-equal convexity (A and B) and unequal to highly unequal convexity (C and D). Specimens shown are (A) *Caribachlamys* cf. *mildredae* (jts 11-B-1, height (ht) = 26.44 mm), (B) Pectinid A *lineolaris* (NMB G 17478, ht = 39.69 mm), (C) *Euvola marensis* (NMB G 17479, ht = 59.92 mm), and (D) *Euvola ziczac* (NMB G 17480, ht = 49.05 mm).

against the log of abundance for each species in the samples (Figure 16). We then divided the field into 4 quadrants defined by the median values of the two axes; high abundance and wide range (upper right), low abundance and wide range (upper left), high abundance and small range (lower right), and low abundance and small range (lower left). Abundance and frequency of occurrence are highly positively correlated as has been commonly observed for other taxa (Jackson, 1974; Cheetham & Jackson, 1996). In both oceans, 45% of the species occur in the upper right quadrant of this plot. Four of the five most frequently occurring species are from the Pacific (squares in Figure 16) whereas the four species found at the lowest percentage of localities are all from the Caribbean (circles in Figure 16). In addition, 7 of the 8 previously undescribed species (solid points) are in the lower left (fewest localities and lowest abundance) quadrant. The eighth species is relatively abundant but not widespread.

DISCUSSION

The problems associated with sampling rare species can have a strong effect on taxonomic practice as revealed by the rare species recorded in this study. First, all of the 8 previously undescribed species are virtually identical to previously described species in the other ocean and are likely geminate species (Table 4). Most of these species are rare. Very similar results were observed for gastropods of the *Strombina* group, for which the numbers of apparent geminate species pairs increased substantially with increased sampling (compare Jung, 1989 with Jackson et al., 1993, 1996). The rarity of one or the other of geminate species pairs likely reflects response to changing environmental conditions since the final separation of the two oceans by the rising Isthmus of Panama.

Second, the rarity of apparent geminate species may sometimes result in the failure to record an entire genus or subgenus from one ocean or the other. For example, the discovery of *Pseudamusium* (*Peplum*) sp. D cf. *P.* (P.) *fasciculatum* (Figure 2M, N) is the first reported occurrence of this genus or sub-genus in the Caribbean.

Third, the rarity of certain taxa may lead taxonomists to mistakenly question the provenance of apparently rogue specimens in old museum collections. For example, *Lindapecten* sp. B cf. *L. acanthodes* (Dall, 1925) in the Pacific and *Spathochlamys* sp. A cf. *S. vestalis* (Reeve, 1853) may actually have been previously described and later discredited due to lack of additional material. Grau (1959) discussed the species *Pecten squarrosus* Carpenter, 1865. Due to the similarity of the type specimen of *P. squarrosus* to *L. acanthodes* in the Caribbean, and the absence of any additional specimens resembling the type specimen in the Eastern Pacific, the name was considered *nomen dubium.* Grau did take into consideration known problems with Carpenter's localities. Our point here is not that this name is in fact valid, but that discrediting of the name based solely on the lack of subsequent material is questionable because so many species are rare.

The occurrence of the species *Spathochlamys* sp. A (Figure 2G, H) in the Caribbean is a similar example.

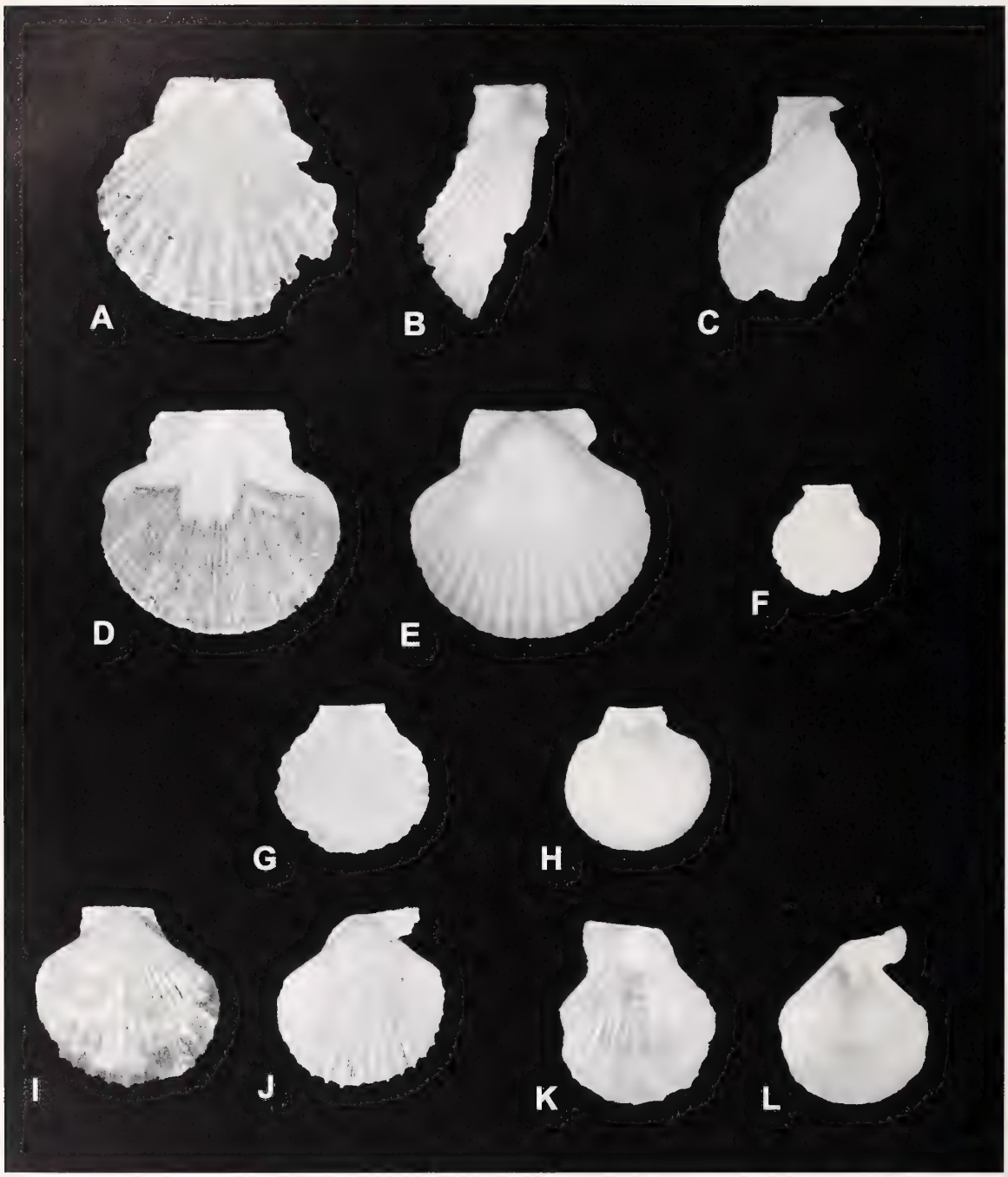


Figure 9. *Euvola, Cryptopecten,* and *Laevichlamys.* (A, B) *Euvola sericeus* (CTPA 405-B-25, (A) lvh = 43.64 mm, (B) rvh = 42.80 mm), (C) *E.* sp. E. (CTPA 326-B-52, rvh = 36.01 mm), (D, E) *E. ziczac* (NMB 17662-B-3, (D) lvh = 47.35 mm, (E) rvh = 49.05 mm), (F) *E.* cf. *raveneli* (CTPA 503-B-115, lvh = 12.4 mm), (G) *E. chazaliei* (CTPA 482-B-4, lvh = 20.05 mm), (H) *E. chazaliei* (CTPA 329-B-9, rvh = 22.8 mm), (I, J) *Cryptopecten phrygium* (NMB G 17481, (I) lvh = 31.58 mm, (J) rvh = 23.8 mm), (K, L) *Laevichlamys multisquamata* (CTPA 579-B-4, (K) lvh = 16.81 mm, (L) rvh = 12.25 mm).

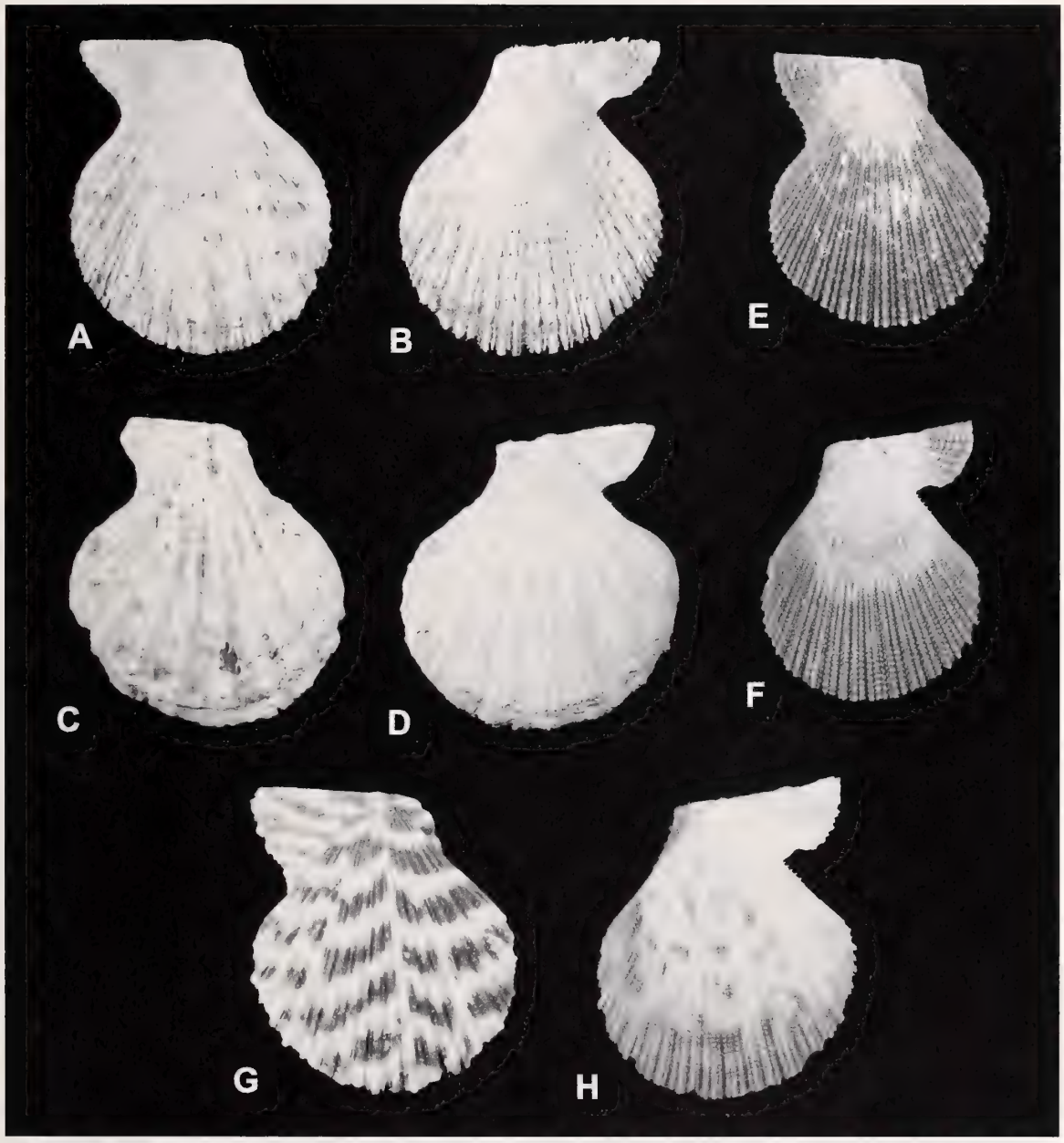


Figure 10. *Caribachlamys*. (A, B) *Caribachlamys* cf. *mildredae* (jts 11-B-1, (A) lvh = 26.5 mm, (B) rvh = 26.58 mm), (C, D) *C. imbricata* (NMB G 17482, (C) lvh = 35.01 mm, (D) rvh = 34.75 mm), (E) *C. sentis* (CTPA 525-B-7, lvh = 13.67 mm), (F) *C. sentis* (CTPA 487-B-89, rvh = 13.66 mm), (G, H) *C. ornata* (NMB G 17483, (G) lvh = 18.39 mm, (H) rvh = 17.74 mm).

Spathochlamys vestalis (Figure 2E, F) was originally described from the West Indies. Waller (1993) determined this locality to be in error, partially based on the resemblance of the type specimen to specimens of *Chlamys lowei* (Hertlein, 1935) from the Gulf of California. Again, Waller did take into account known locality errors within Reeve's collection. However, the discovery of *Spathochlamys* sp. A in the Caribbean may in fact indicate that the original locality data was not in error. This would necessitate the use of the name *Spathochlamys vestalis* for the Caribbean species, and *Spathochlamys lowei* for the eastern Pacific species. We are not advocating this nomenclatural change in this paper, only again emphasizing the dangers associated with making assumptions regarding geographic distributions based on faunas that have not been sampled sufficiently.

A final similar example concerns *Caribachlamys* cf. *mildredae* (Figure 10A, B) that was recently collected by

Table 2

Occurrences of all species reported from the CTPA samples and used in this study. The occurrences are reported as number of localities/number of specimens. The second column (Figure) refers to the figure number illustrating the specimen in this paper. Regions cited are (GC) Gulf of Chriqui, Panama, (GP) Gulf of Panama, Panama, (LCH) Cochinos Cays, Honduras, (CMN) Mosquito Cays, Nicaragua, (BT) Bocas del Toro, Panama, (BA) Almirante Bay, Panama, (LC) Chriqui Lagoon, Panama, (GM) Gulf of Mosquitoes, Panama, and (SB) San Blas, Panama.

Taxa	Figure	GC	GP	LCH	CMN	BT	BA	LC	GM	SB	Total
Argopecten gibbus (Linnaeus, 1758)	6 c, d	—	—	12/86	10/251	3/3	3/4	3/9	—	15/50	46/403
Argopecten ventricosus (Sowerby II, 1842)	6 e, f	33/1087	25/196	—	—	—	—	—	—	—	58/1283
Bractechlamys antillarum (Recluz, 1853)	2 k, l	—	—	7/9	5/12	11/41	5/70	8/80	9/34	4/9	55/311
Bractechlamys sp. H	2 o, p	3/7	—	—	—	—	—	—	—	—	3/7
Caribachlamys imbricata (Gmelin, 1791)	10 c, d	—	—	3/3	1/1	5/8	2/2	3/6	—	1/1	17/33
Caribachlamys sentis (Reeve, 1853)	10 e, f	—	—	2/3	2/2	4/7	3/4	5/8	1/1	1/1	19/27
Euvola cf. raveneli (Dall, 1898)	9 f	—	—	1/1	—	4/9	2/4	—	—	1/1	8/15
Euvola chazaliei (Dautzenberg, 1900)	9 g, h	—	—	11/61	8/17	14/124	2/58	6/48	12/426	10/17	64/752
Euvola laurenti (Gmelin, 1791)	12 c, d	—	—	5/11	5/15	8/25	4/5	19/165	6/14	5/16	53/252
Euvola perulus (Olsson, 1961)	12 e, f	14/65	17/45	—	—	—	—	—	—	—	31/110
Euvola sericeus (Hinds, 1845)	9 a, b	4/22	1/1	—	—	—	—	—	—	—	5/23
Euvola sp. E	9 c	—	—	1/1	—	—	—	—	—	—	1/1
Euvola sp. F	12 g, h	—	—	—	—	4/10	1/2	1/1	4/8	—	10/21
Euvola ziczac (Linnaeus, 1758)	9 d, e	—	—	2/2	3/3	3/3	—	3/4	1/3	—	17/46
Laevichlamys multisquamata (Dunker, 1864)	9 k, l	—	—	3/5	—	3/5	—	—	5/20	1/1	12/31
Leptopecten bavayi (Reeve, 1852)	13 g, h	—	—	3/4	3/3	6/12	5/7	5/6	3/6	2/3	30/62
Leptopecten biolleyi (Hertlein and Strong, 1946)	13 a, b	29/1243	21/380	—	—	—	—	—	—	—	50/1623
Leptopecten sp. C	13 c, d	—	—	—	—	7/42	3/9	1/1	2/24	—	13/76
Leptopecten velero (Hertlein, 1935)	13 e, f	6/12	—	—	—	—	—	—	—	—	6/12
Lindapecten acanthodes (Dall, 1925)	11 a, b	—	—	14/30	10/65	6/59	3/33	8/18	5/48	9/15	62/379
Lindapecten sp. B	11 c, d	2/3	2/3	—	—	—	—	—	—	—	4/6
Nodipecten arthriticus (Reeve, 1853)	3 d, e	9/31	—	—	—	—	—	—	—	—	9/31
Nodipecten nodosus (Linnaeus, 1758)	3 a, b	—	—	4/4	6/6	1/2	—	—	1/1	8/10	24/49
Nodipecten sp. G	3 c	—	—	—	—	3/5	1/2	1/1	—	—	5/8
Pacipecten leucophaeus (Reeve, 1852)	13 k	—	—	—	—	2/2	—	—	—	—	2/2
Pacipecten linki (Dall, 1926)	13 l, m	—	—	1/3	3/5	6/49	3/7	8/19	4/36	2/2	27/121
Pacipecten tumbezensis (d'Orbigny, 1846)	13 i, j	28/487	23/126	—	—	—	—	—	—	—	51/613
Pectinid A *lineolaris* (Lamarck, 1819)	6 a, b	—	—	7/31	5/11	19/388	7/106	16/351	18/468	10/35	84/1416
Pseudamusium (*Peplum*) *fasciculatum* (Hinds, 1845)	2 i, j	7/35	2/5	—	—	—	—	—	—	—	9/40
Pseudamusium (*Peplum*) sp. D	2 m, n	—	—	1/1	2/2	2/2	—	2/5	2/3	—	9/13
Spathochlamys benedicti (Verrill and Bush, 1897)	2 a, b	—	—	10/27	6/15	14/101	4/80	8/40	10/94	12/45	64/402
Spathochlamys sp. A	2 g, h	—	—	—	—	2/11	—	1/2	1/1	—	4/14
Spathochlamys vestalis (Reeve, 1853)	2 e, f	20/82	20/85	—	—	—	—	—	—	—	40/167
Total Richness		11	8	17	14	21	15	17	16	14	33
Total Localities		42	35	18	13	27	16	30	27	22	230

Table 3

Measures of Diversity. Values are given for all 9 regions sampled in this study and combined as oceans for comparison. Richness is the number of species, H is the Shannon-Weiner Index, and α is Fisher's Alpha. H and α are calculated as described in the text.

Region	Richness	H	α
All Caribbean Samples	22	2.1188	3.0477
Cochinos Cays, Honduras	17	2.0679	3.9760
Mosquito Cays, Nicaragua	15	1.4470	3.0575
Almirante Bay, Panama	15	1.9501	3.0989
Bocas del Toro, Panama	21	2.0257	3.8361
Chiriqui Lagoon, Panama	17	1.7113	3.0812
Gulf of Mosquitoes, Panama	16	1.5847	2.6138
San Blas, Panama	14	2.1150	3.3667
All Eastern Pacific Samples	11	1.4103	1.3840
Gulf of Chiriqui, Panama	11	1.3788	1.4340
Gulf of Panama, Panama	8	1.4303	1.2242

Table 4

Geminate species pairs. We are considering 9 groups of species to be geminate species pairs. All but 1 of these pairs includes a previously undescribed species. Undescribed species are indicated using open nomenclature as discussed in the text.

Pacific geminate	Caribbean geminate
Bractechlamys sp. H	*Bractechlamys antillarum*
Euvola sericeus	*Euvola* sp. E
Euvola perulus	*Euvola* sp. F
Leptopecten velero	*Leptopecten bavayi*
Leptopecten biolleyi	*Leptopecten* sp. C
Lindapecten sp. B	*Lindapecten acanthodes*
Nodipecten arthriticus	*Nodipecten* sp. G
Pseudamusium (*Peplum*) *fasciculatum*	*Pseudamusium* (*Peplum*) sp. D
Spathochlamys vestalis	*Spathochlamys* sp. A

snorkeling in 2 meters water depth from the Bocas del Toro region of Panama, and therefore not included in analyses of the dredge samples. Numerous other specimens were observed living attached to branching corals and additional specimens have been identified from private collections in the region (Kim Hutsell, personal communication, 2001). Olsson and McGinty (1958) reported the species *C. mildredae* from Bocas del Toro, well outside its previously reported geographic range. Cahill (1990) discredited this report based on his inspection of several specimens from the San Blas Archipelago finding

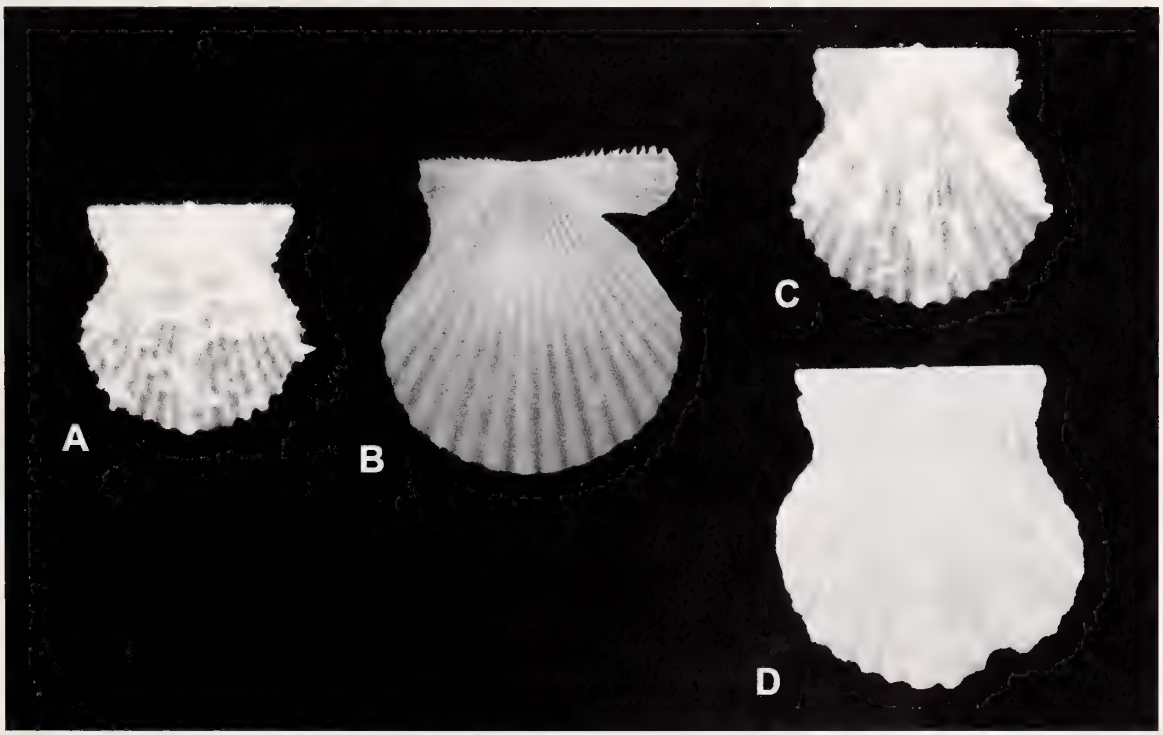


Figure 11. *Lindapecten*. (A) *Lindapecten acanthodes* (CTPA 334-B-5, lvh = 4.92 mm), (B) *L. acanthodes* (CTPA 445-B-3, rvh = 13.88 mm), (C) *L.* sp. B (CTPA 394-B2, lvh = 5.16 mm), (D) *L.* sp. B (CTPA 399-B-147, lvh = 10.53 mm).

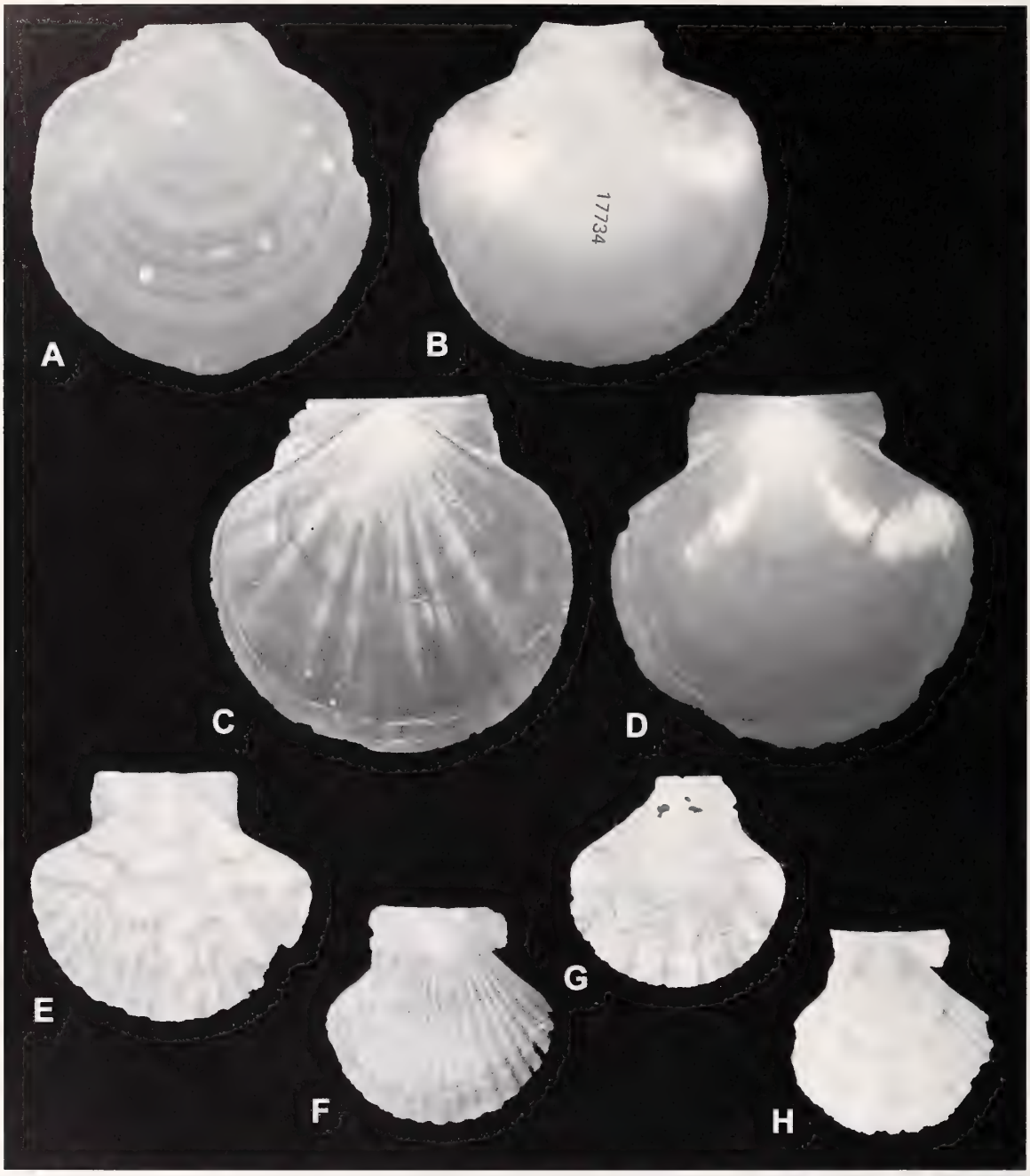


Figure 12. *Euvola.* (A, B) *Euvola marensis* (NMB G 17479, (A) left valve height (lvh) = 59.92 mm, (B) right valve height (rvh) = 57.91 mm), (C, D) *E. laurenti* (CTPA 494-B-11, (C) lvh = 61.31 mm, (D) rvh = 64.38), (E) *E. perulus* (CTPA 378-B-77, lvh = 21.33 mm). (F) *E. perulus* (CTPA 368-B-100, rvh = 28.71 mm), (G, H) *E.* sp. F (CTPA 534-B-62, (G) lvh = 17.38 mm, (H) rvh = 17.85 mm).

that these specimens were variants of *Caribachlamys imbricata* (Gmelin, 1791) and specimens of that variant were most likely the basis for Olsson and McGinty's report. However, our discovery indicates that Olsson and McGinty most likely did sample this species although it may not be *C. mildredae.* It is apparently intermediate between *C. imbricata* and *C. mildredae.* Once again, extensive sampling is essential before one ascribes too much taxonomic importance to the absence of specimens from collections.

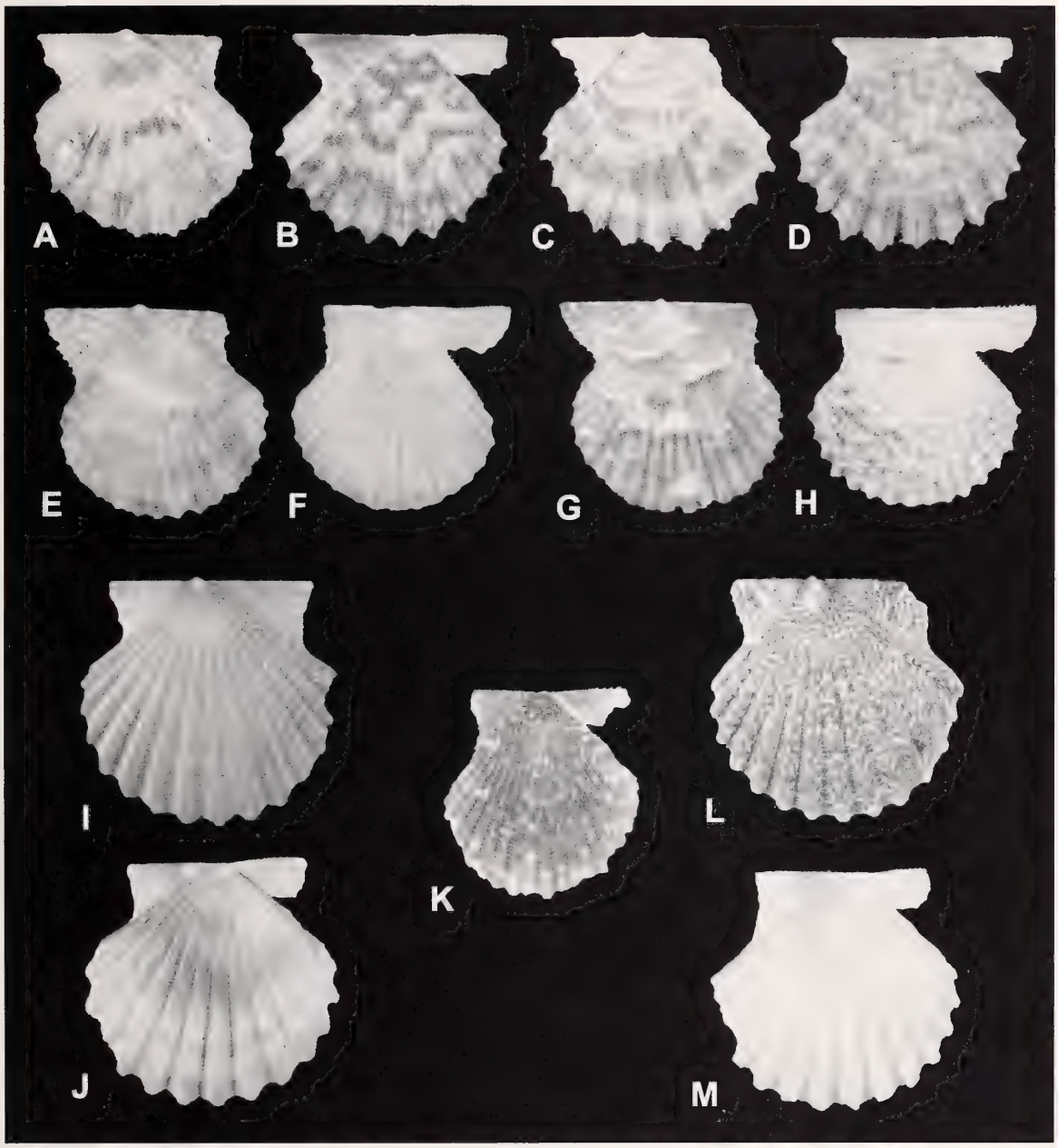


Figure 13. *Leptopecten* and *Pacipecten*. (A, B) *Leptopecten biolleyi* (CTPA 465-B-169, (A) lvh = 10.31 mm, (B) rvh = 8.72 mm), (C, D) *L.* sp. C (CTPA 485-B-111, (C) lvh = 10.06 mm, (D) rvh = 10.41 mm), (E, F) *L. velero* (CTPA 407-B-172, (E) lvh = 8.78, mm (F) rvh = 7.33 mm), (G, H) *L. bavayi* (CTPA 556-B-46, (G) lvh = 8.61 mm, (H) rvh = 8.49 mm), (I, J) *Pacipecten tumbezensis* (CTPA 421-B-67, (I) lvh = 20.62 mm, (J) rvh = 24.83 mm), (K) *P. leucophaeus* (CTPA 533-B-76, rvh = 7.52 mm), (L) *P. linki* (CTPA 337-B-49, lvh = 15.14 mm), (M) *P. linki* (CTPA 538-B-58, rvh = 15.34 mm).

CONCLUSIONS

The numbers of species of scallops in the southwestern Caribbean is more than double that in the tropical Eastern Pacific. However, the magnitude of differences observed across the Isthmus depends greatly on the frequency and spatial scale of sampling. Numbers of species from individual large samples are similar in the two oceans because the much greater abundance of specimens in the Pacific masks the actual differences in regional diversity. These differences are consistent with the much higher primary production by phytoplankton and greater food availability for suspension feeders in the tropical Eastern Pacific (Birkeland, 1977, 1987; Coates et al., 1996;

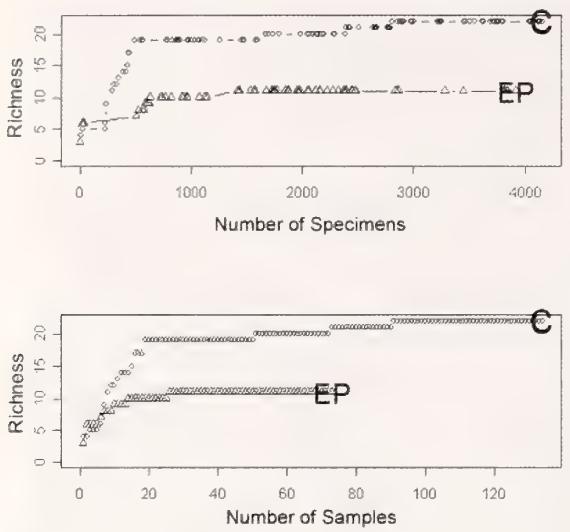


Figure 14. Species richness. Plots of species richness shown as cumulative sampling curves for both number of specimens (upper plot) and number of samples (lower plot). Diversity is plotted as species richness for the Caribbean (C) and the Eastern Pacific (EP).

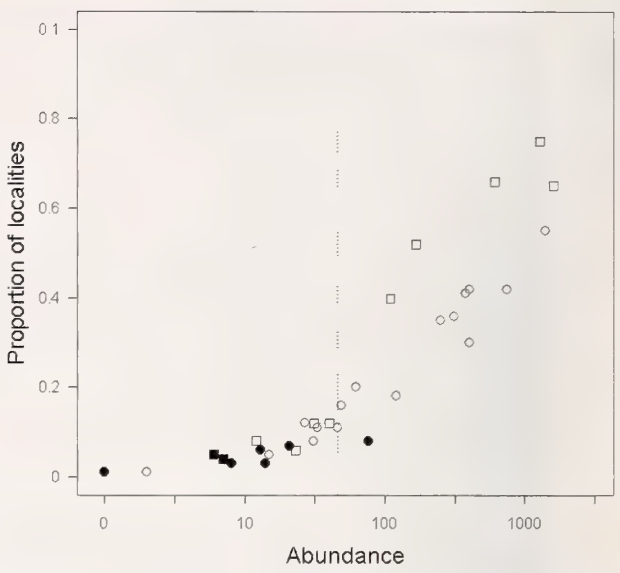


Figure 16. Abundance vs. geographic range. Pacific species represented by squares and the Caribbean fauna by circles. Previously undescribed species shown as solid points.

D'Croz and Robertson, 1997; Jackson & D'Croz, 1998). Numbers of species from the different regions sampled are consistently about one and one half times greater in the Caribbean regions compared to the Eastern Pacific, and even higher at Bocas del Toro. However, many Caribbean species occur in only a fraction of the regions sampled, as compared with the broader distribution of Eastern Pacific species. This is because of the much greater differences in environmental conditions such as the relative abundance of well developed coral reefs and sea grass meadows among the Caribbean regions. Thus, the full differences in diversity are only apparent after intensive sampling from all the regions combined, and even this is almost certainly inadequate for collecting all the species present.

These effects of sampling scale are summarized in Figure 17, showing the relationship between numbers of species encountered and the geographic area (numbers of

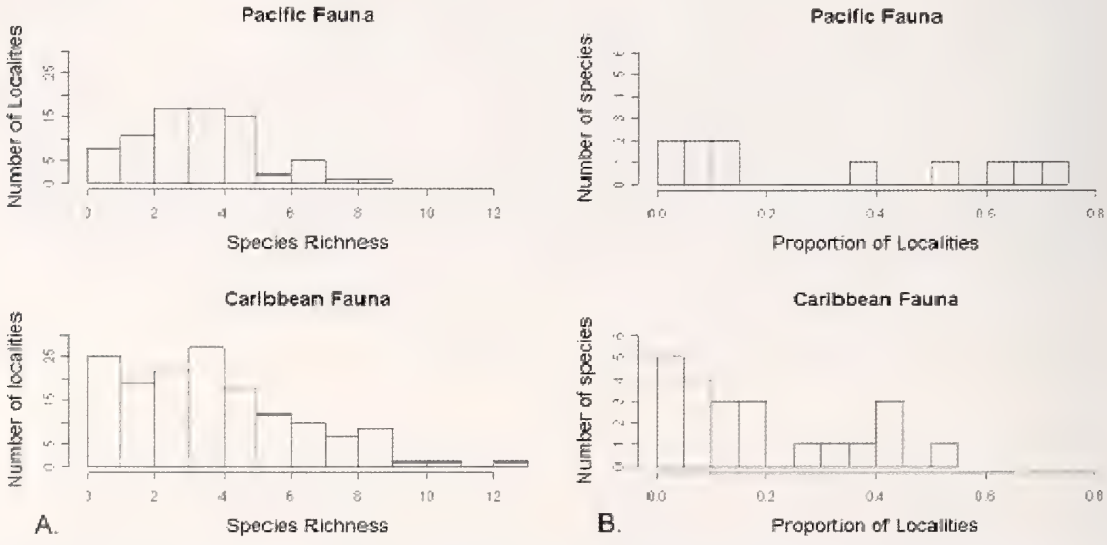


Figure 15. Commonness and abundance of tropical scallops. Upper plots represent the Pacific fauna and the lower plots the Caribbean. (A) Histogram of species richness by locality. (B) Histogram of proportion of localities of occurrence. Proportion is plotted as opposed to absolute numbers of localities to normalize for unequal sampling effort.

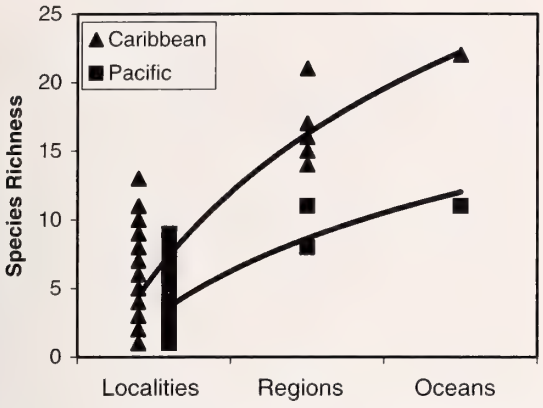


Figure 17. Species area plot. The x-axis represents 3 distinct "geographical" values: locality, region, and ocean. The y-axis plots the number of species found. Points do not depict the distribution of values, only the ranges. The lines were plotted as a simple best-fit model using Excel.

regions) sampled. The curves describe a general logarithmic fit to the data from each ocean in the form of sampling effort curve. Despite the larger number of regions sampled, the Caribbean curve is still rising steeply in comparison to the Eastern Pacific. In some ways this is analogous to Whitaker's (1972) measurement of beta diversity. The alpha (local) diversity is roughly the same in either ocean, which very likely explains the considerable previous confusion about patterns of diversity across the Isthmus. Beta (regional) diversity is more difficult to quantify, but in this analysis it can be crudely approximated as the slope of the line as the geographic range is expanded from locality to region to ocean. This slope is much higher in the Caribbean than in the Eastern Pacific. The gamma (ocean) diversity is clearly higher in the Caribbean, although considerably more sampling is needed in both the Eastern Pacific and southwest Caribbean to more accurately estimate the magnitude of difference across the Isthmus.

Acknowledgments. Sampling could not have been completed without the assistance and expertise of the crew of the *RV Urraca* and the staff of the NAOS Marine Laboratory. Preparation and processing of the dredge samples was accomplished through the efforts of Marcos Alvarez and Felix Rodriquez at CTPA. Jon Todd outlined the initial taxonomic identification protocols used by the PPP. Ken Johnson provided invaluable assistance in analyses, fieldwork in the Dominican Republic, and management of the research collection and data. Kim Hutsell provided valuable comment on taxonomic identification and observations of private collections from the region. Peter Roopnarine and an anonymous reviewer provided valuable feedback on an earlier version of the manuscript.

We thank the government of the Republic of Panama for the permits allowing such a large-scale sampling program. Fieldwork was funded by two separate Scholarly Studies Grants from the Smithsonian Institution to Jeremy Jackson and Helena Fortunato. Funding for the use of the scanning electron microscope at SIO was provided by a student research grant from the Western Society of Malacology.

LITERATURE CITED

Abbott, R. T. & P. A. Morris. 1995. A Field Guide to Shells: Atlantic and Gulf Coasts and the West Indies. Houghton Mifflin: Boston, Massachusetts. 350 pp.

Allmon, W. D., G. Rosenberg, R. W. Portell & K. S. Schindler. 1993. Diversity of Atlantic coastal plain mollusks since the Pliocene. Science 260:1626–1629.

Allmon, W. D., G. Rosenberg, R. W. Portell & K. S. Schindler. 1996. Diversity of Pliocene-Recent mollusks in the western Atlantic: extinction, origination, and environmental change. Pp. 271–302 in J. B. C. Jackson, A. F. Budd & A. G. Coates (eds.), Evolution and Environment in Tropical America. University of Chicago Press: Chicago, Illinois.

Barucca, M., E. Olmo, S. Schiaparelli & A. Canapa. 2004. Molecular phylogeny of the family Pectinidae (Mollusca: Bivalvia) based on mitochondrial 16S and 12S rRNA genes. Molecular Phylogenetics and Evolution 31(1):89–95.

Bayer, F. M., G. L. Voss & C. R. Robbins. 1970. Report on the marine fauna and benthic shelf-slope communities of the isthmian region. Bioenvironmental and radiological-safety feasibility studies Atlantic-Pacific interoceanic canal, IOCS Memorandum BMI-41.

Birkeland, C. 1977. The importance of the rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proceedings, 3rd International Coral Reef Symposium, Miami, 15–21.

Birkeland, C. 1987. Nutrient availability as a major determinant of differences among coastal hard-substratum communities in different regions of the tropics. Pp. 43–98 in C. Birkeland (ed.), Comparison between Atlantic and Pacific Tropical Marine Coastal Ecosystems: Community Structure, Ecological Process, and Productivity. UNESCO Report on Marine Science Vol. 46. UNESCO, Paris, France.

Budd, A. F. 2000. Diversity and extinction in the Cenozoic history of Caribbean reefs. Coral Reefs 19(1):25–35.

Buzas, M. A., C. F. Koch, S. J. Culver & N. F. Sohl. 1982. On the distribution of species occurrences. Paleobiology 8(2): 143–150.

Buzas, M. A. & S. J. Culver. 1991. Species diversity and dispersal of benthic foraminifera. BioScience 41(7):483–489.

Cahill, M. 1990. The Pectinidae of the Caribbean coast of Panama. American Conchologist 18:7–8.

Canapa, A., M. Barucca, A. Marinelli & E. Olmo. 2000. Molecular data from the 16s rRNA gene for the phylogeny of Pectinidae (Mollusca: Bivalvia). Journal of Molecular Evolution 50:93–97.

Cheetham. A. H. & J. B. C. Jackson. 1996. Speciation, extinction, and the decline of arborescent growth in Neogene and Quaternary Cheilostome Bryozoa of Tropical America. Pp. 205–233 in J. B. C. Jackson, A. F. Budd & A. G. Coates (eds.), Evolution and Environment in Tropical America. University of Chicago Press: Chicago, Illinois.

Cheetham, A. H. & J. B. C. Jackson. 2000. Neogene history of Cheilostome Bryozoa in Tropical America. Proceedings of the 11th International Bryozoology Association Conference: 1–16.

Chesher, R. H. 1972. The status of knowledge of Panamanian echinoids, 1971, with comments on other echinoderms. Bulletin, Biological Society of Washington 2:139–158.

Coan, E. V., P. V. Scott & F. R. Bernard. 2000. Bivalve seashells of western North America: Marine bivalve mollusks

from Arctic Alaska to Baja California. Santa Barbara Museum of Natural History Monographs Number 2. 763 pp.

Coates, A. G. & J. A. Obando. 1996. The geologic evolution of the Central American Isthmus. Pp. 21–56 in J. B. C. Jackson, A. F. Budd & A. G. Coates (eds.), Evolution and Environment in Tropical America. University of Chicago Press: Chicago, Illinois.

Coates, A. G., J. B. C. Jackson, L. S. Collins, T. M. Cronin, H. J. Dowsett, L. M. Bybell, P. Jung & J. A. Obando. 1996. Closure of the Isthmus of Panama: the near-shore marine record of Costa Rica and western Panama. Geological Society of America 104:814–828.

Coates, A. G., M. P. Aubry, W. A. Berggren, L. S. Collins, and M. Kunk. 2003. Early Neogene history of the Central American arc from Bocas del Toro, western Panama. Geological Society of America Bulletin 115(3):271–287.

Collins, L. S. 1999. The Miocene to recent diversity of Caribbean benthic foraminifera from the Central American Isthmus. Bulletins of American Paleontology 357:91–107.

D'Croz, L. & D. R. Robertson. 1997. Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. Pp. 2053–2058 in H. A. Lessios, and I. G. McIntyre (eds.), Proc. 8th Inter. Coral Reef Symposium Vol. 2. Smithsonian Tropical Research Institute, Balboa, Panama.

Ekdale, A. A. 1974. Marine mollusks from shallow-water environments (0 to 60 meters) off the Northeast Yucatan coast, Mexico. Bulletin of Marine Science 24(3):639–668.

Espinosa, J., J. Ortea & A. Valdes. 1994. Catalogue of the recent bivalve molluscs from the Cuban Archipelago. Avicennia 2:109–129.

Fortunato, H. 1998. Reconciling observed patterns of temporal occurrence with cladistic hypotheses of phylogenetic relationship. American Malacological Bulletin 14:191–200.

Frischer, M. E., J. Williams & E. Kenchington. 1998. A molecular phylogeny of some major groups of Pectinidae inferred from 18s rRNA gene sequences. Pp 213–221 in P. A. Johnston and J. W. Haggart (eds.), Bivalves: An Eon of Evolution. University of Calgary Press: Calgary, Alberta, Canada.

Gaston, K. J. 1994. Rarity. Chapman and Hall, London.

Grau, G. 1959. Pectinidae of the eastern Pacific. Allan Hancock Expeditions 23: 308 pp.

Humfrey, M. 1975 Seashells of the West Indies. Collins, St. James Place, London.

Jackson, J. B. C. 1974. Biogeographic consequences of eurytopy and stenotropy among marine bivalves and their evolutionary significance. The American Naturalist 108(962):541–560.

Jackson, J. B. C., P. Jung, A. G. Coates & L. S. Collins. 1993. Diversity and extinction of tropical American mollusks and emergence of the Isthmus of Panama. Science 260:1624–1625.

Jackson, J. B. C., P. Jung & H. Fortunato. 1996. Paciphilia revisited: transisthmian evolution of the *Strombina* group (Gastropoda: Columbellidae). Pp. 234–270 in J. B. C. Jackson, A. F. Budd & A. G. Coates (eds.), Evolution and environment in tropical America. University of Chicago Press: Chicago, Illinois.

Jackson, J. B. C. and J. D'Croz. 1998. The ocean divided. Pp. 38–71 in A. G. Coates (ed.), Central America: A Natural and Cultural History, Yale University Press: New Haven, Connecticut.

Jackson, J. B. C., J. A. Todd, H. Fortunato & P. Jung. 1999. Diversity and assemblages of Neogene Caribbean Mollusca of lower Central America. Bulletins of American Paleontology 357:193–230.

Johnson, K. G. & T. McCormick. 1995. STATPOD: Statistical Analysis of Palaeontological Occurrence Data, Version 0.1. Computer program distributed by the Department of Geology and Applied Geology, University of Glasgow, United Kingdom.

Jones, D. F. & P. F. Hasson. 1985. History and development of the marine invertebrate faunas separated by the central American isthmus. Pp. 325–355 in F. G. Stehli & S. D. Webb (eds.), The Great American Biotic Interchange. Plenum Press: New York.

Jung, P. 1989. Revision of the *Strombina*-group (Gastropoda: Columbellidae), fossil and living. Schweizerische Palaontologische Abhandlung, 111:1–298.

Keen, A. M. 1971. Sea Shells of Tropical West America. Stanford University Press: Stanford, California. 1064 pp.

Kidwell, S. M. 2001. Preservation of species abundances in marine death assemblages. Science 294:1091–1094.

Kidwell, S. M. 2002a. Time-averaged molluscan death assemblages: palimpsets of richness, snapshots of abundance. Geology 30(9):803–806.

Kidwell, S. M. 2002b. Mesh-size effects on the ecological fidelity of death assemblages: a meta-analysis of molluscan live-dead studies. Geobios Special Memoir 24:107–119.

Knowlton, N., L. A. Weight, L. A. Solórzano, D. K. Mills & E. Berningham. 1993. Divergence in proteins, mitochondrial DNA, and reproductive compatibility across the Isthmus of Panama. Science 260:1629–1631.

Knowlton, N. & L. A. Weight. 1998. New dates and new rates for divergence across the Isthmus of Panama. Proceedings, Royal Society of London, Series B: Biological Sciences 265(1412):2257–2263.

Lessios, H. A. 1990. Adaptation and phylogeny as determinants of egg size in echinoderms from two sides of the Isthmus of Panama. The American Naturalist 135:1–13.

Matsumoto, M. & I. Hayami. 2000. Phylogenetic analysis of the family Pectinidae (Bivalvia) based on mitochondrial cytochrome c oxidase subunit 1. Journal of Molluscan Studies 66:477–488.

Merlano, J. M. D. & M. P. Hegedus. 1994. Molluscos del Caribe Colombiano. Fundación Natura: Bogota, Columbia. 291 pp.

Mikkelsen, P. M. & R. Bieler. 2000. Marine bivalves of the Florida Keys: discovered biodiversity. Pp. 367–397 in E. M. Harper & J. A. Crame (eds.), The Evolutionary Biology of the Bivalvia. Geological Society of London, Special Publications 177.

Moore, E. J. 1984. Tertiary marine pelyecypods of California and Baja California: Propeamussiidae and Pectinidae. United States Geological Survey Professional Paper 1228-B:112 p.

Olsson, A. A. 1961. Mollusks of the Tropical Eastern Pacific. Paleontological Research Institution: Ithaca, New York. 574 pp.

Olsson, A. A. & T. L. McGinty. 1958. Recent marine mollusks from the Caribbean coast of Panama with the description of some new genera and species. Bulletins of American Paleontology 39:1–58.

Petuch, E. J. 1995. Molluscan diversity in the Late Neogene of Florida: evidence for a two-staged mass extinction. Science 270:275–277.

Rabinowitz, D. 1981. Seven forms of rarity. Pp. 205–217 in H. Synge (ed.), The Biological Aspects of Rare Plant Conservation. Wiley: New York.

RADWIN, G. E. 1969. A recent molluscan fauna from the Caribbean coast of southeastern Panama. San Diego Society of natural History, Transactions 15(14):229–236.

REDFERN, C. 2001. Bahamian Seashells, A Thousand Species for Abaco, Bahamas. Bahamianseashells.com, Boca Raton, Florida.

RIOS, E. C. 1985. Seashells of Brazil. Fundação Cidade do Rio Grande: Rio Grande, Brazil. 328 pp.

ROOPNARINE, P. D. 2001. A history of diversification, extinction, and invasion in tropical America as derived from species-level phylogenies of *Chionine* genera (family Veneridae). Journal of Paleontology 75:644–657.

ROY, K., D. JABLONSKI & J. W. VALENTINE. 2000. Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. Proceedings, Royal Society of London, Series B 267:293–299.

SMITH, J. T. 1991. Cenozoic giant pectinids from California and the Tertiary Caribbean province: *Lyropecten,* "*Macrochlamis*", *Vertipecten,* and *Nodipecten* species. United States Geological Survey Professional Paper 1391:155 pp.

STANLEY, S. M. & L. D. CAMPBELL. 1981. Neogene mass extinctions of western Atlantic mollusks. Nature 293:457–459.

STEINER, G. & M. MULLER. 1996. What can 18s rDNA do for bivalve phylogeny. Journal of Molecular Evolution 43:58–70.

VERMEIJ, G. J. 1978. Biogeography and Adaptation: Patterns of Marine Life. Harvard University Press: Cambridge, Massachusetts. 332 pp.

VERMEIJ, G. J. 1993. The biological history of a seaway. Science 260:1603–1604.

VERMIEJ, G. J. & E. J. PETUCH. 1986. Differential extinction in tropical American mollusks: endemism, architecture, and the Panama land bridge. Malacologia 27:29–41.

VERON, J. E. N. 2000. Corals of the World. Australian Institute of Marine Science. Townsville, MC, Qld, Australia. 1382 pp.

VOKES, H. E. & E. H. VOKES. 1983. Distribution of shallow-water marine Mollusca, Yucatan Peninsula, Mexico. Mesoamerican Ecology Insititute Monograph 1, Middle American Research Institute Publication 54: 183 p. Tulane University, New Orleans, Louisiana.

WALLER, T. R. 1969. The evolution of the *Argopecten gibbus* stock (Mollusca: Bivalvia), with emphasis on the Tertiary and Quaternary species of Eastern North America. The Paleontological Society Memoir 3:1–125.

WALLER, T. R. 1973. The habits and habitats of some Bermudian marine mollusks. The Nautilus 87:31–52.

WALLER, T. R. 1986. A new genus and species of scallop (Bivalvia: Pectinidae) from off Somalia, and the definition of a new tribe Decatopectinini. The Nautilus 100:39–46.

WALLER, T. R. 1991. Evolutionary relationships among commercial scallops (Mollusca: Bivalvia: Pectinidae). Pp 1–73 in S. E. Shumway (ed.), Scallops: Biology, Ecology and Aquaculture. Elsevier: New York, New York.

WALLER, T. R. 1993. The evolution of "*Chlamys*" (Mollusca: Bivalvia: Pectinidae) in the tropical western Atlantic and eastern Pacific. American Malacological Bulletin 10:195–249.

WHITAKER, R. H. 1972. Evolution and measurement of species diversity. Taxon 21(2/3):215–251.

WOODRING, W. P. 1966. The Panama land bridge as a sea barrier. Proceedings of the American Philosophical Society 110: 425–433.

The Veliger 48(1):46–60 (June 30, 2006)

THE VELIGER

Additions and Refinements to Aptian to Santonian (Cretaceous) *Turritella* (Mollusca: Gastropoda) from the Pacific Slope of North America

RICHARD L. SQUIRES

Department of Geological Sciences, California State University, Northridge, California 91330-8266, USA

AND

LOUELLA R. SAUL

Invertebrate Paleontology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, USA

Abstract. This paper presents the first detailed paleontologic study of pre-Campanian (pre-late Late Cretaceous) *Turritella* sensu lato from the Pacific slope of North America, mainly from outcrops in California. Seven species, two of which are new, have a cumulative chronologic range of late Aptian to Santonian, an interval of 30 million years that coincides with much of Chron C34, the long-normal interval. One of the new species, *Turritella* ***xylina***, is only the second known Cenomanian *Turritella* from the study area, and the other new species, *Turritella* ***encina***, is the first Santonian *Turritella* reported from the study area. The previously named species are redescribed and are refined in their stratigraphic distributions. They are: *Turritella seriatimgranulata* Roemer, 1849, of late Aptian age; *Turritella infralineata* Gabb, 1864, of late early Albian age; *Turritella petersoni* Merriam, 1941, Cenomanian to early Turonian age; *Turritella hearni* Merriam, 1941, of Turonian and probably Coniacian age; and *Turritella iota* Popenoe, 1937, of late Turonian age. *Turritella seriatimgranulata* is also known from Albian strata in Sonora, Mexico, New Mexico, and Texas.

INTRODUCTION

The shallow-marine gastropod *Turritella* Lamarck, 1799, is common in the uppermost Cretaceous (Campanian and Maastrichtian) through Pleistocene rock record of the Pacific slope of North America. Stemming from the work by Marwick (1957b), many workers have subdivided *Turritella* into other genera and subgenera, and these subdivisions relied on morphologic characters such as the outer lip trace, ontogeny of the primary spirals, and protoconch. Kaim (2004), however, reported that until a thorough review of this genus is done, shell characters cannot be of use for taxonomic purposes above the species level. Lacking this review of turritellas, we refer these species described in this present paper to *Turritella sensu lato.*

Turritellas have been well studied and used with much success for biostratigraphic zonation of the Campanian through Pleistocene rock record of the study area (e.g., Grant & Gale, 1931; Loel & Corey, 1932; Merriam, 1941; Weaver, 1943; Givens, 1974; Saul, 1983a, b; Squires, 1987), but the pre-Campanian record of *Turritella* has received far less study. Reports of pre-Campanian *Turritella* from this region are based mainly on the works of Gabb (1864), Merriam (1941), and Allison (1955). In the last 50 years, however, knowledge of the Pacific slope of North America Cretaceous stratigraphy has increased significantly, and much more collecting has been done. This present study, which expands on the foundation provided by early workers, is based on collections borrowed from all the major museums having extensive collections of Cretaceous fossils from the Pacific slope of North America. We detected 56 lots: 29 at California Academy of Sciences (CAS), 23 at Los Angeles County Natural History Museum, Invertebrate Paleontology (LACMIP), and 4 at University of California Museum of Paleontology, Berkeley (UCMP). These lots were collected mostly from California, and a few were collected from northern Baja California (Figure 1). We found specimens that yielded new morphologic information, and we more fully establish the geologic ranges and geographic/stratigraphic distributions of the five previously named species. In addition, we detected two new species. This study establishes the late Aptian to Santonian record of *Turritella* from California and the northern part of Baja California, Mexico. This interval of geologic time coincides with Chron C34, the long-normal interval (Figure 2). Hereafter, these *Turritella* will be referred to as the "long normal" turritellas. The significance of this study is that *Turritella* can be used for biostratigraphic purposes in working with pre-Campanian rocks.

The shallow-marine, warm-water aspect of the studied species of *Turritella* is generally analogous to the ecology of Recent *Turritella.* A sampling of the literature shows that most species of Recent *Turritella* prefer shallow-ma-

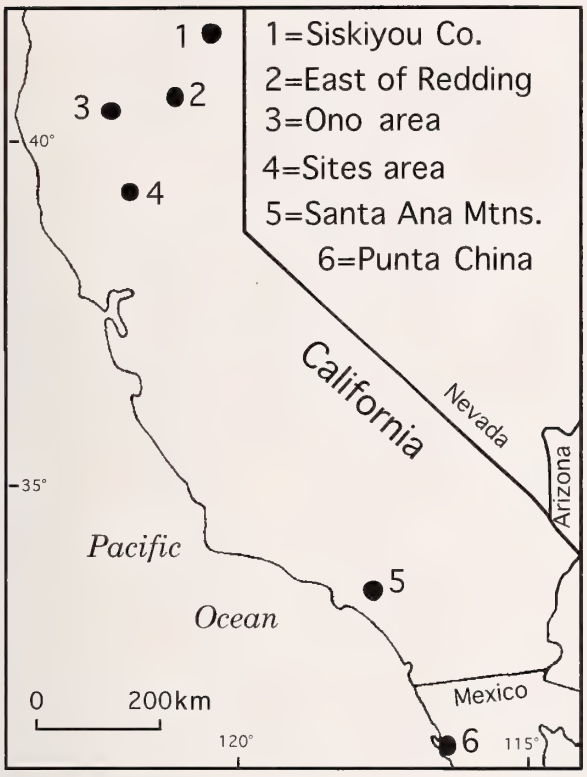


Figure 1. Index map showing locales mentioned in the text.

rine depths between low intertidal and approximately 100 m, even though they have been found in waters as deep as 1500 m (Thorson, 1957; Yonge & Thompson, 1976; Squires, 1984; Saul, 1983a; Allmon, 1988). Recent *Turritella* prefer relatively warm temperatures between 15 and 20°C, although they can live in temperatures between 2 and 24°C (Allmon, 1988). They are, however, specifically more diverse and individually of larger size in the tropics than those found in temperate seas (Merriam, 1941). Most modern-day species are largely sedentary and infaunal/semi-infaunal in relatively soft substrate, but many are also mobile and epifaunal on coarser or harder substrates (Yonge & Thompson, 1976). Some species usually remain immobile for long periods of time, shallowly buried in soft, level-bottom substrates, then voluntarily crawl to more sandy bottoms or bottoms covered with gravel in order to spawn (Bandel, 1976; Yonge & Thompson, 1976; Allmon et al., 1992). Most modern-day species of *Turritella* appear to be ciliary suspension feeders, but some or all might be deposit feeders or grazers at least part of the time (Allmon, 1988; Allmon et al., 1992). They can also be extremely gregarious, with up to approximately 500 individuals per square meter (Merriam, 1941; Petuch, 1976). Information on the mode of development is known (see Marwick, 1957b, Richter & Thorson, 1975, and Bandel et al., 1997) for only a few living species of *Turritella*. Pelagic larval phases are relatively short for these species and range from two days to three weeks (Allmon, 1988).

Figure 3 shows the notational system used here to designate the spiral sculpture. This system, which is based on the work of Marwick (1957a), is explained in the caption for Figure 3.

Abbreviations, other than those cited above, that are used for catalog and locality numbers are: CIT, California Institute of Technology, Pasadena; UCLA, University of California, Los Angeles (collections now housed at LACMIP); USNM, United States National Museum, Washington, D.C.

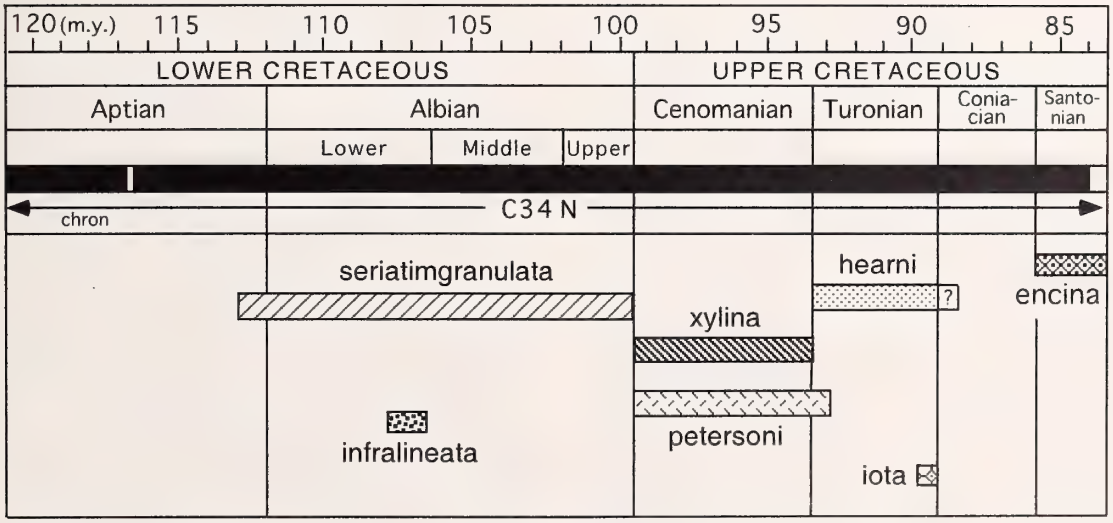


Figure 2. Chronostratigraphic positions of the new and restudied Cretaceous turritellas. Ages of stage boundaries and magnetostratigraphy data from Gradstein et al. (2004:fig. 19.1).

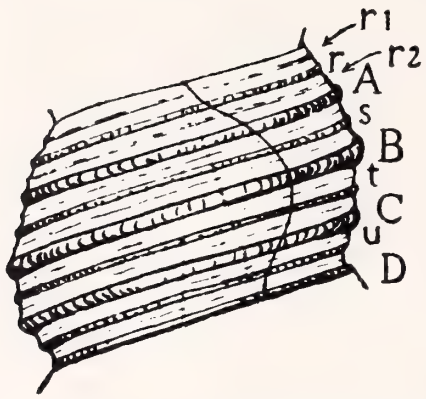


Figure 3. Diagram showing notation of spiral ribs of *Turritella.* Primary ribs are denoted A, B, C, and D; secondary ribs are denoted by r, s, t, and u; and tertiary threads are denoted by r_1, r_2, etc. Change in relative rib strength shown by exchanging upper for lower case letters (i.e., capital letters for strong ribs and lower case for weaker ribs). (Diagram modified from Marwick, 1957a:fig. 1).

STRATIGRAPHY

The geologic ages and depositional environments of most of the Pacific slope of North America formations and members cited in this paper have been summarized in papers by Saul (1982) and Squires & Saul (2003a, b, 2004a, b). These ages range from late Aptian through Santonian, and the depositional environments are usually shallow marine, with post-mortem displacement of some of the shallow-marine faunas into deeper waters via turbidity currents. Stratigraphic information mentioned below concerns those rock units not discussed in recent literature.

Cretaceous Rocks Near Yreka

The holotype of *Turritella hearni* Merriam, 1941, was reported by Merriam (1941:64) as having been collected ". . . from the Turonian at the type locality near Montague and Yreka . . .," both of which are in Siskiyou County, northern California. Montague is approximately 8 km slightly southeast of Yreka. Although Merriam never specifically mentioned whether the type locality is at Montague or Yreka, Anderson (1958:153) reported the locality to be in middle Turonian beds on the Hagerdorn Ranch, 6.4 km north of Montague. Museum labels in the box that contains the holotype have two locations cited: one at 6.4 km north of Montagu and one 13 km northeast of Yreka. The label that has the official CAS locality number (61938) is the former location. Matsumoto (1960: 97) indicated the beds 6.4 km north of Montague to be Coniacian in age, based on a few ammonites. Utilizing the outcrop map of Sliter et al. (1984:figs. 1, 2), beds in the area just north of Montague (i.e., the Black Mountain area) plot in the lower Coniacian part of the Hornbrook Formation and are probably part of the Ditch Creek Siltstone Member. Sliter et al. (1984) based their geologic age on the ammonite *Prionocycloceras* sp. These same workers, however, reported that just southwest of the Black Mountain area, there are extensive covered intervals and small discontinuous outcrops of sandstone and siltstone which cannot be correlated to the exact member of the Hornbrook Formation. The age of the beds at the type locality of *T. hearni,* therefore, cannot be positively determined, but the age is probably early Coniacian.

Turritella hearni is also present in the extension of the Hornbrook Formation in Turonian strata (LACMIP loc. 25272) near Phoenix, Jackson County, southwestern Oregon. For a discussion of the age of the strata in this area, see Squires & Saul (2004b).

Lower Part of Tuna Canyon Formation

Turritella iota Popenoe, 1937, is reported here for the first time from the lower part of the Tuna Canyon Formation west of Rustic Canyon in the east-central Santa Monica Mountains, Los Angeles County, southern California. The specimens are from coarse-grained sandstone at LACMIP loc. 26967 in the basal part of the formation. Overlying the basal part is a black-shale unit containing scaphitoid-ammonites (Popenoe, 1973; Almgren, 1973; Colburn, 1973). Alderson (1988), based on ammonites, reported that the black-shale unit is late Turonian to Coniacian age and that the underlying coarse-grained sandstone beds (i.e., those containing *T. iota*) are late Turonian in age and are coeval to the upper Baker Canyon and the lower Holz Shale members of the Ladd Formation in the Santa Ana Mountains, Orange County, southern California. Prior to this present paper, *Turritella iota* had only been found in the lower Holz Shale Member of the Ladd Formation; thus, the presence of *T. iota* in the Santa Monica Mountains strengthens the age equivalency of these parts of these two formations.

BIOGEOGRAPHIC IMPLICATIONS

The earliest known records of *Turritella* are from the Early Cretaceous (early Valanginian) of Poland (Schröder, 1995; Kaim, 2004) and the Valanginian of France (d'Orbigny, 1842). The earliest known record of *Turritella* on the Pacific slope of North America is *Turritella seriatimgranulata* Roemer, 1849. It occurs in the Tethyan gastropod- and bivalve-rich fauna (Allison, 1955, 1974) of the upper Aptian Alisitos Formation, northern Baja California, Mexico, and this species is described and illustrated in this present report. The arrival of *Turritella* onto the Pacific slope of North America during the late Aptian coincided with both a global trend of rising sea level (Haq et al., 1987) and with warm and equable surface waters (Frakes, 1999).

During the Albian through Turonian, warm-water conditions existed on the Pacific slope of North America

(Saul, 1986). Shallow-water Albian strata are not plentiful in the study area, and most of the shallow-water Albian mollusks contained in these strata are from redeposited blocks. During the Albian, *T. seriatimgranulata* migrated into New Mexico, Texas, and Sonora, Mexico. Although surface currents were predominantly westward-flowing during the Aptian and Albian in the southern part of North America, there were substantial eastward-flowing surface currents (see Johnson, 1999:figs. 2, 3) that could have transported the larvae of *T. seriatimgranulata* eastward from the westward part of Mexico.

The Turonian coincided with widespread warm seas that were at their highest sea-level stand of the Cretaceous (Haq et al., 1987; Frakes, 1999), and the Turonian coincided with the peak in diversity for *Turritella* species in the study area, with collectively three species present (Figure 2). Two of these species, *T. petersoni* and *T. hearni,* had the widest geographic distribution of all the studied species.

Relative to the Turonian, the Coniacian to early Campanian had a slightly cooler climate (Frakes, 1999), and only a moderately high sea-level stand (Haq et al., 1987). The boundaries of the Tethyan Realm were generally broadest during the Aptian to Turonian and the narrowest during the Coniacian to Maastrichtian (Sohl, 1987). These more restrictive conditions might help explain why there is only a single known species, *Turritella* ***encina*** sp. nov., of limited geographic distribution, known from the study area during the interval represented by the Coniacian and Santonian. The paucity of exposures of shallow-water Coniacian strata in California accounts for the scarcity of Coniacian turritellas.

Superorder CAENOGASTROPODA Cox, 1959
Order NEOTAENIOGLOSSA Haller, 1882
Family TURRITELLIDAE Lovén, 1847
Genus *Turritella* sensu lato Lamarck, 1799

Type species: *Turbo terebra* Linneaus, 1758, by monotypy; Recent, western Pacific.

Diagnosis: Shell small to large, turreted-conical, many whorled, elongate, slender, sculptured with spiral ribs and/or threads, growth lines curved, aperture round and entire, outer lip thin, sinuous and prosocline at suture, columella smooth and concave, operculum horny and multispiral (after Davies, 1971:309).

Discussion: The growth lines, noded ribs, and early whorl sculpture of six of the seven turritellas treated in this paper (i.e., *T. seriatimgranulata, T. infralineata, T. petersoni, T. hearni, T. iota,* and *T.* ***encina***) are similar. On the basis of shell characteristics, none of these "long normal" turritellas resembles the most common Campanian-Maastrichtian turritella stock of *Turritella chicoensis* Gabb, 1864. Very early whorls of *T. chicoensis* stock appear bicostate (ribs B and C) although the peribasal spiral D is present, and the whorls become quadricostate (A, B, C, D) by the eight whorl. Early whorls of seventh turritella treated in this paper (i.e., *T.* ***xylina***) are unavailable, but adult whorls resemble those of *Turritella chaneyi* Merriam, 1941, stock.

Turritella seriatimgranulata Roemer, 1849
(Figures 4–7)

Turritella seriatim-granulata Roemer, 1849:413; 1852:39, pl. 4, figs. 12a, 12b; Gabb, 1869:263; Stanton, 1947: 75–76, pl. 56, figs. 7, 11, 17–24; Almazan-Vazquez, 1990:159, pl. 1, fig. 8; Akers & Akers, 1997:93, fig. 78.

Not *Turritella seriatim-granulata* Roemer. Gabb, 1864:132, pl. 20, fig. 88 (two views: natural size and magnified) = tentatively, *Turritella packardi* Merriam *fide* Saul (1983a:102–104).

Not *Turritella seriatimgranulata* Roemer. Stewart, 1927: 348–349, pl. 21, fig. 2 = tentatively, *Turritella packardi* Merriam *fide* Saul (1983a:102–104).

Not *Mesalia seriatim-granulata* (Roemer). Shimer & Shrock, 1944:495, pl. 203, figs. 3, 4.

Turritella marnochi White, 1879:314, pl. 7, fig. 5b (not 5a).

Turritella vibrayeana d'Orbigny. Böse, 1910:145, pl. 30, fig. 10; pl. 31, fig. 6.

Turritella macropleura Stainbrook, 1940:712, pl. 33, figs. 17, 20–21.

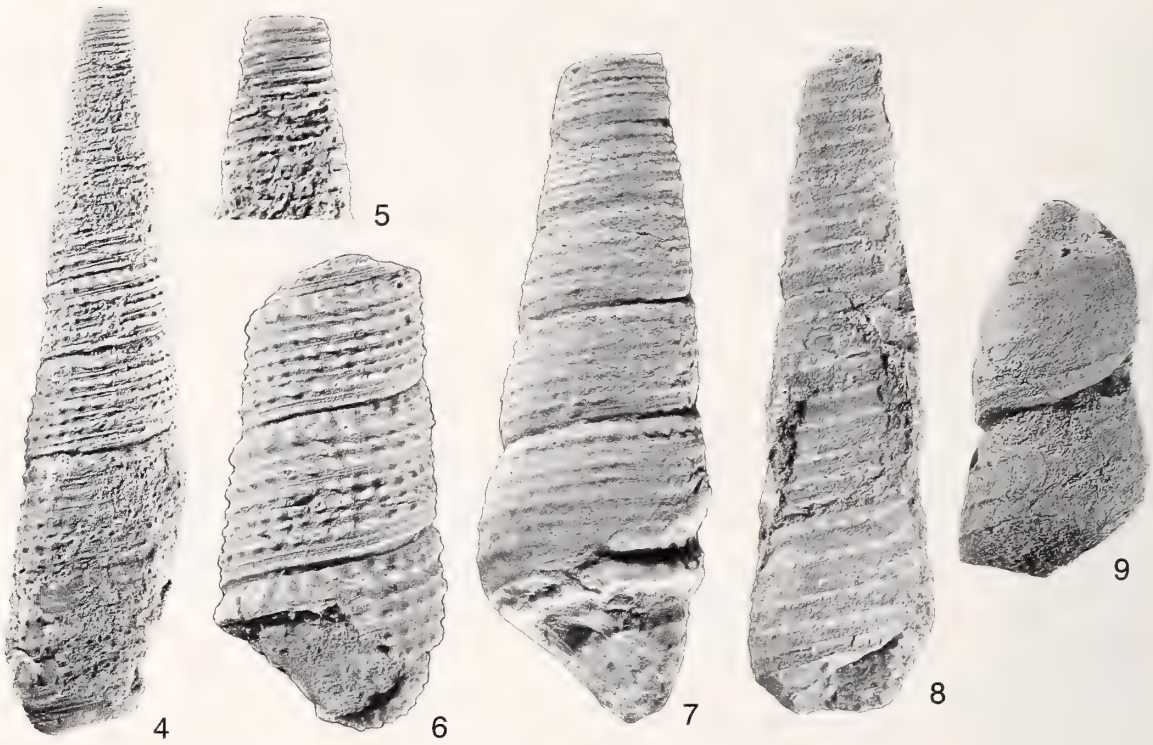
Mesalia (*Mesalia*) *mauryae* Allison, 1955:414–415, pl. 41, fig. 3.

Turritella (*Haustator*) aff. *T.* (*H.*) *seriatimgranulata* Roemer. Allison, 1955:415, pl. 41, fig. 5.

Diagnosis: Adult whorls generally flat sided, with five nearly equal-strength spiral ribs, closely spaced, noded, and alternating with finer noded ribs; R strongest and carina-like. Interspaces with unnoded threads.

Description: Shell medium-large (up to 90 mm, estimated, in height), slender. Pleural angle narrow (15°). Protoconch and earliest juvenile whorls unknown. Teleoconch whorls approximately 15 to 17, flat-sided; posteriormost part of whorls with slightly rounded profile. Late-juvenile whorls (approximately 1.75 mm diameter) with four (R, A, B, and C) nearly equal and squarish ribs, interspaces deep and smooth and about same width as ribs. Adult whorls (approximately 5 mm diameter and greater) with five (R, A, B, C, and D) spiral ribs, nearly equal in strength (R strongest, projecting and somewhat carina-like), equidistant, noded, and alternating with weaker ribs (also noded); resulting in sculpture pattern R, r_2, A, s, B, t, C, u, and D. Rib r_1 occasionally present, approaching R in strength, with nodes on both ribs nearly merging. Nodes variable in strength, weakest on D. Threads on all interspaces, very thin, variable in number (three to six), and unnoded; threads most numerous on interspace between B and C, and C and D. Suture deep. Aperture round, inner lip can have thin callus pad. Base of last whorl with unnoded spiral ribs.

Holotype: USNM 103148.



Explanation of Figures 4 to 9

Figures 4–9. Specimens coated with ammonium chloride. Figures 4–7. *Turritella seriatimgranulata* Roemer, 1849. Figures 4–5. Hypotype UCMP 156008, UCMP loc. A-9521. Figure 4. Abapertural view, ×3.5. Figure 5. Tip of specimen shown in Figure 4, ×8.7. Figure 6. Hypotype UCMP 156009, UCMP loc. A-9521, right-lateral view, ×4. Figure 7. Hypotype UCMP 156010, from near Arivechi, northern Sonora, Mexico, apertural view, ×2.5. Figures 8–9. *Turritella infralineata* Gabb, 1864, CAS loc. 69104. Figure 8. Neotype CAS 69286, apertural view, ×3.4. Figure 9. Hypotype CAS 69287, abapertural view, ×3.1.

Type locality: Either the Walnut Creek or Comanche Peak formation near Fredericksburg, Gillespie County, south-central Texas (Stanton, 1947:76).

Geologic age: Late Aptian to late Albian.

Distribution: UPPER APTIAN: Alisitos Formation, marine part of upper member, Punta China region, northern Baja California, Mexico. APTIAN-ALBIAN UNDIFFERENTIATED: Morita Formation, Cerro las Conchas, near Ariveachi, Sonora, Mexico. UPPER LOWER ALBIAN: Washita and Fredericksburg Groups, Texas. UPPER ALBIAN: Pawpaw Formation, Texas; Purgatorie Formation, Mesa Tucumcari, New Mexico.

Discussion: This study of *T. seriatimgranulata* is based on approximately 1000 specimens from the Alisitos Formation near Punta China (UCMP loc. A-9521) and two specimens from the Morita Formation near Arivechi. The Alisitos material consists entirely of the tips of specimens, and the preservation is very good.

Poorly preserved small fragments of *Turritella* identified as *T. seriatimgranulata* Roemer in Gabb (1864) and Stewart (1927) from Tuscan Springs, Tehama County, northern California were tentatively regarded by Saul (1983a:102–104) to be *Turritella packardi* Merriam, 1941, which is of early to possibly middle Campanian age.

Shrimer & Shrock (1944) refigured both the natural-size view and the magnified view of Gabb's (1864:pl. 20, fig. 88) specimen and identified it as *Mesalia seriatimgranulata.*

Mesalia (*Mesalia*) *mauryae* Allison, 1955, is known only from one locality in the Alisitos Formation. This locality is where *T. seriatimgranulata* is also found. *Mesalia* (*M.*) *mauryae* is known only from tips of specimens, and their sculpture is identical to that of the tips of some specimens (see Figure 5) of *T. seriatimgranulata.* For this reason, we believe *M.* (*M.*) *mauryae* to be a synonym of *T. seriatimgranulata.*

Gabb (1869:263) reported specimens of *T. seriatimgranulata* from the Morita Formation near Arivechi, Sonora, Mexico. Stanton (1947:76, pl. 56, figs. 17, 18, 23, 24) stated that these Mexican specimens appear to be within the form range of *T. seriatimgranulata,* and he provided illustrations of two specimens of Gabb's original lot.

Comparison of specimens (see Figure 7) of *T. seriatimgranulata* from the Morita Formation near Arivechi with those from Punta China confirmed that this species occurs at these two locales. All the Punta China specimens, however, are just the tips of this species. At Arivechi, specimens are up to 60 mm in height and are missing their tips. We estimate that complete specimens of *T. seriatimgranulata* would be approximately 90 mm in height. Akers & Akers (1997) reported that Texas specimens of this species are up to at least 62 mm in height, and Stanton (1947:75) reported that an average specimen, with the apex restored, would be approximately 70 mm in height.

The age range of the formations in Texas containing *T. seriatimgranulata* is late early Albian to late Albian, according to Akers & Akers (1997); the age of the Purgatorie Formation in New Mexico is late early Albian, according to Cobban & Reeside (1952); and the age of the Morita Formation in northern Mexico is undifferentiated Aptian-Albian, according to Almazan-Vazquez (1990).

Turritella infralineata Gabb, 1864
(Figures 8–9)

Turritella infralineata Gabb, 1864:131–132, pl. 20, fig. 87; Stewart, 1927:291; Merriam, 1941:65, pl. 1, fig. 13 (refigure of Gabb, 1864).

Turritella cf. *T. hearni* Merriam. Rodda, 1959:123–124 (unfig.).

Diagnosis: Adult whorls generally flat-sided, with four to five, nearly equal-strength spiral ribs (C strongest and can be slightly carina-like), widely spaced and weakly noded; interspaces bearing numerous threads.

Description: Shell medium, slender. Pleural angle narrow (11°). Protoconch and juvenile whorls unknown. Teleoconch with flat-sided to weakly concave whorls. Early adult whorls (approximately 5 mm diameter) with four (R, A, B, and C) nearly equal ribs, weakly noded, and separated by wide interspaces bearing numerous unnoded threads; C strongest and somewhat carina-like. Adult whorls with five (R, A, B, C, and D) nearly equal ribs, R and C strongest, with C usually somewhat carina-like. Ribs s and u occasionally somewhat prominent on later whorls. Suture impressed. Aperture round. Base of last whorl unknown. Growth line deeply sinused, sigmoidal with antispiral sinus between A and B ribs.

Neotype: CAS 69286 (designated herein).

Neotype locality: CAS loc. 69104.

Geologic age: Late early Albian, *Brewericeras hulenense* ammonite zone.

Distribution: Budden Canyon Formation, Chickabally Mudstone Member, Texas Springs area, Shasta County, northern California.

Discussion: This study of Gabb's species is based on 49 specimens, all from the Texas Springs area. Preservation is mostly very poor, but at CAS loc. 69104 some of the specimens show moderately good preservation.

According to Stewart (1927:291) and Merriam (1941: 65), the holotype of *Turritella infralineata* is lost. A neotype (Figure 8) is chosen here.

Gabb (1864:131–132) reported *Turritella infralineata* from the North Fork of Cottonwood Creek area, Shasta County, northern California and from Orestimba Canyon, Stanislaus County, northern California. His locality description for the Cottonwood Creek locality is stratigraphically imprecise because this fork of the creek cuts through the entire Budden Canyon Formation, which ranges in age from Hauterivian to Turonian (see Murphy et al., 1969:pl. 1). The probable stratigraphic position of Gabb's locality, however, was determined during this present investigation, based on specimens matching the original description of *T. infralineata* from the general vicinity of the North Fork of Cottonwood Creek in the Chickabally Mudstone Member of the Budden Canyon Formation at Texas Springs in the Ono area (Figure 1, locale 3). This member is of late early Albian age and correlative to the ammonite *Brewericeras hulenense* zone (see Squires & Saul, 2004b). Texas Springs is approximately 12 km northeast of the North Fork of Cottonwood Creek area. *Turritella infralineata* occurs at several localities in the Texas Springs area, and a total of 16 specimens were detected. The largest specimen is 35 mm in height, but it is incomplete. Preservation is generally poor, but a few good specimens, including the neotype, are from CAS loc. 69104.

We were not able to confirm Gabb's (1864) report of the occurrence of *T. infralineata* from Orestimba Canyon, Stanislaus County, and we were not able to make definite identifications of many of the fossils from this area. The canyon cuts across rocks ranging from Jurassic? and Early Cretaceous to early Tertiary age, and detailed field studies are needed in this area before any definitive biostratigraphic work can be done.

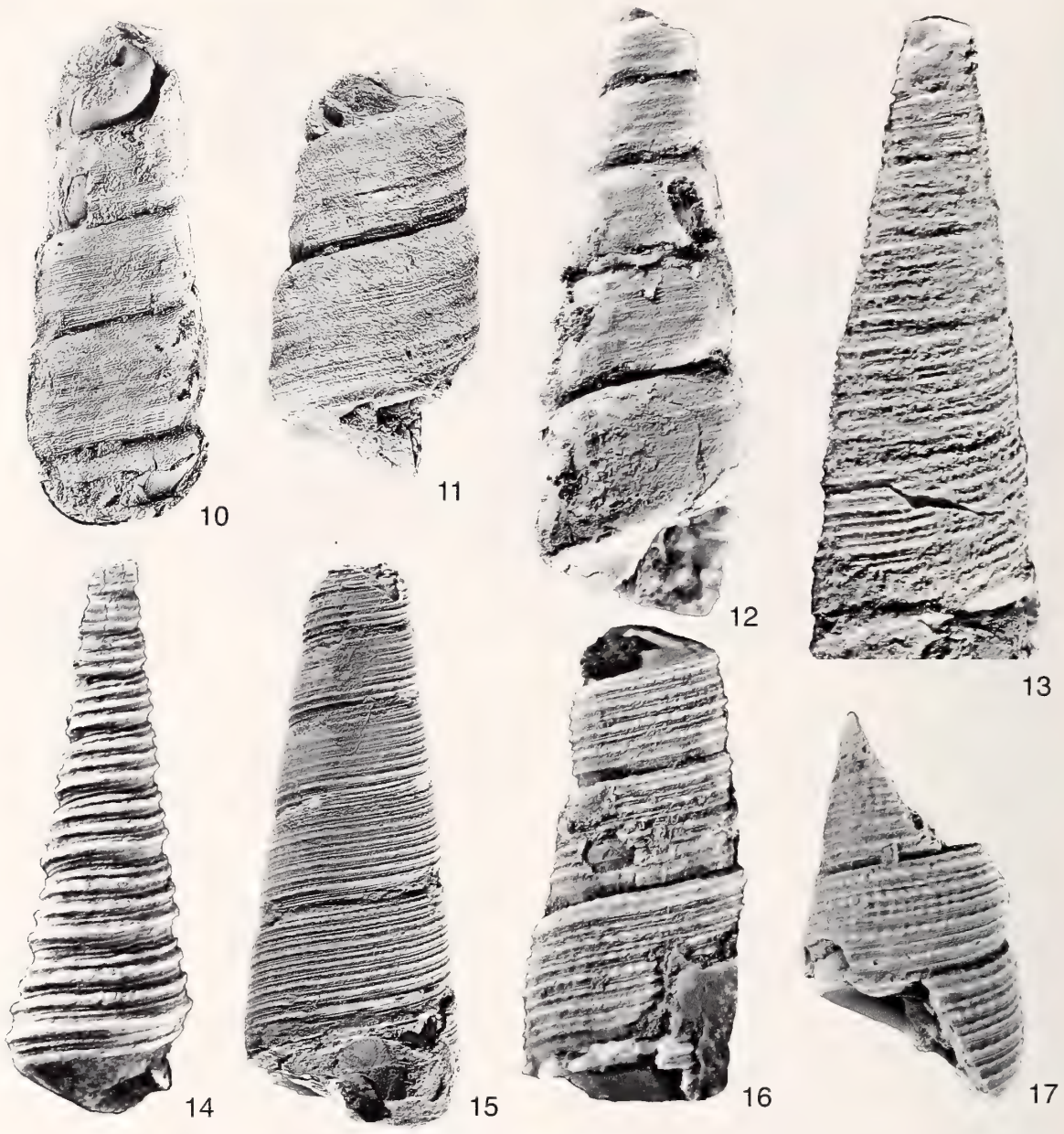
Turritella infralineata resembles *T. hearni,* but *T. infralineata* differs by having much weaker nodes and much wider interspaces.

Turritella ***xylina*** Squires & Saul, sp. nov.
(Figures 10–12)

Turritella cf. *T. robertiana* (Anderson). Rodda, 1959:124; Murphy & Rodda, 1960:text-fig. 2.

Diagnosis: Adult whorls with concave middle part flanked by shoulder and abapical angulations. Sculpture generally subdued, consisting only of numerous spiral threads.

Description: Shell medium (estimated 40 mm total height). Protoconch and early juvenile whorls unknown. Pleural angle 18°. Early adult whorls (approximately 4.5



Explanation of Figures 10 to 17

Specimens coated with ammonium chloride. Figures 10–12. *Turritella* ***xylina*** Squires & Saul, sp. nov. Figure 10. Holotype CAS 69111.02, CAS loc. 69111, right-lateral view, ×2.9. Figure 11. Paratype LACMIP 13315, LACMIP loc. 27242, abapertural view, ×2.5. Figure 12. Paratype LACMIP 13316, LACMIP loc. 23470, apertural view, ×4. Figures 13–17. *Turritella petersoni* Merriam, 1941. Figure 13. Holotype CAS 1291.06, CAS loc. 1291, left-lateral view, ×6.1 Figure 14. Hypotype CAS 69106.02, CAS loc. 69106, apertural view of tip, ×8.8. Figure 15. Hypotype CAS 69107.05, CAS loc. 69107, apertural view, ×2.2. Figure 16. Hypotype CAS 69284, CAS loc. 2335, abapertural view, ×3.9. Figure 17. Hypotype CAS 69285, CAS loc. 69098, right-lateral view, ×2.5.

to 5 mm diameter) slightly convex, covered by spiral threads of generally uniform strength. Adult whorls (approximately 5 mm diameter and greater) concave between very broad and flattened shoulder area and broad to moderately sharp abapical angulation (rib C?); medial part of concave part of whorl commonly bears moderately prominent rib B? and several threads. Suture impressed. Growth line sigmoidal, antispiral on concave part of whorl.

Dimensions of holotype: 24 mm in height, 9 mm greatest diameter (specimen incomplete).

Holotype: CAS 69111.02.

Type locality: CAS 69111, 122°33′30″W longitude, 40°27′15″N latitude.

Paratypes: LACMIP 13315 and 13316.

Geologic age: Cenomanian.

Distribution: Budden Canyon Formation, Bald Hills Member, North Fork Cottonwood Creek, Shasta County, northern California.

Discussion: This new species is based on 38 specimens, and preservation is only moderately good. The largest specimen is 34 mm in height and 13.5 mm in greatest diameter, but the specimen is incomplete.

Turritella ***xylina*** is unlike the other species described in this present paper. It most closely resembles *Turritella chaneyi orienda* Saul (1983a:84–86, pl. 5, figs. 4–11, 16–17) from upper Maastrichtian strata in central and southern California. *Turritella* ***xylina*** differs by having a wider pleural angle, overall weaker ribbing (especially on the concave middle part of the whorls), shoulder closer to suture with narrow interwhorl valley, and whorls sides more vertical with stronger shoulder offset, producing a slightly stepped-whorl appearance.

Rodda (1959) identified the new species as *Turritella* cf. *T. robertiana* (Anderson, 1958). Anderson (1958) had originally referred his species to *Nerinea robertiana,* but, as mentioned in Saul & Squires (1998:465), Anderson's specimens are not nerineids. Saul (1983a) mentioned that *T. robertiana* is similar to *T. chaneyi orienda.* She also mentioned that *T. robertiana* is similar to *T. chaneyi* Merriam, 1941, and tentatively included Anderson's supposed nerineid in synonymy with *T. chaneyi.*

Etymology: The species is named for its occurrence in the North Fork Cottonwood Creek area; Greek, *xylinos* meaning of wood.

Turritella petersoni Merriam, 1941
(Figures 13–17)

Turritella petersoni Merriam, 1941:64–65, pl. 1, figs. 10, 11.

Diagnosis: Adult whorls slightly convex to flattish with ribs thin, numerous, weakly noded, closely spaced, and alternating in strength.

Description: Medium shell. Pleural angle approximately 18°. Protoconch unknown. Early juvenile whorls (approximately 1 mm diameter) convex and bearing ribs r, A, B, and C; interspaces as wide as ribs. Juvenile whorls (1 to 4 mm diameter) convex and bearing ribs r, A, s, B, t, C, u, and d; r approaching strength of A, B, and C on whorls approximately 3 mm diameter); A, B, and C weakly noded. Adult whorls (approximately greater than 5 mm diameter) slightly convex to flattish (occasionally with slightly tabulate shoulder) and with numerous, thin, very closely spaced, weakly noded ribs, and alternating in strength with weaker ribs. Occasional specimens (see Figure 17) with R, s, A, B c, u, and d distinguishable, but notation of spiral ribs usually difficult. Threads most common on anterior part of whorls. Some specimens with numerous cycles of single strong rib alternating with bands containing one to four weaker ribs; stronger ribs usually with nodes, weaker ribs unnoded. Suture at but not overlapping d. Area baseward of d with 2 to 3 fine, faintly beaded riblets; bordered by a stronger rib; followed by weak to stronger alternations of diminishing strength to whorl center. Growth line sigmoidal, maximum of antisinus near midpoint of whorl. Aperture round.

Holotype: CAS 1291.06.

Type locality: "1 mile east of Peterson's ranch house, 4 miles north of Sites, Colusa County, California" (Merriam, 1941:64).

Geologic age: Cenomanian to early Turonian.

Distribution: CENOMANIAN: Great Valley Group, Sites area, Colusa County, northern California; Budden Canyon Formation, Bald Hills Member, Ono area, Shasta County, northern California. CENOMANIAN OR TURONIAN: Valle Group, Cedros Island, Baja California, Mexico. LOWER TURONIAN: Budden Canyon Formation, Gas Point Member, lower part, Ono area, Shasta County, northern California.

Discussion: This study of Merriam's species is based on 149 specimens. Preservation is generally good. Many of the specimens are from the Gas Point Member of the Budden Canyon Formation.

Turritella petersoni has been a poorly known species prior to this study. Its geologic age was tentatively reported as Cenomanian by Saul (1978:38–39) because of inexact knowledge regarding the location of its type locality.

Three moderately well preserved specimens of *T. petersoni* were detected from LACMIP loc. 15741 in the Valle Group, Cedros Island, Baja California, Mexico. The specimens are float derived from this group, and utilizing the geologic map provided by Kilmer (1984), the specimens are from either the upper part of the lower member (i.e., the Cenomanian Vargas Formation) or the lower part of the upper member (i.e., the Turonian Pinos Formation).

Turritella petersoni is similar to *Turritella iota* but *T. petersoni* differs by having whorls sides that can be weakly convex (never concave) and in not having a moderate carina at C. *Turritella petersoni* also has more numerous and more closely spaced ribs with the nodes usually stronger, and the sculpture can also vary from ribs having

nodes to ribs without almost any nodes. The latter variation might be due to ecologic factors. The basal sculpture differs from *T. iota* in having ribs of alternating strength.

Turritella hearni Merriam, 1941
(Figures 18–21)

Turritella hearni Merriam, 1941:64, pl. 1, figs. 1–9; Saul: 1982:72 (chart).
Turritella tolenasensis Merriam, 1941:62, pl. 1, figs. 14, 15; Saul, 1983a:103.

Diagnosis: Whorls slightly convex with three prominent and equal-strength spiral ribs (nodes not strong) on juvenile whorls, increasing to four prominent spiral ribs (nodes strong and elongate) on later whorls (ribs A and B strongest) and numerous unnoded threads on all interspaces.

Description: Shell medium. Pleural angle 13°. Protoconch and earliest juvenile whorls unknown. Whorls slightly convex to flattish. Juvenile whorls (less than 4 mm diameter) with ribs A, B, and C equally prominent and unnoded; ribs r and d weak (see Figure 21). Later whorls (greater than 4 mm diameter) show ribs R, A, B, C, t, and d; ribs A and B most prominent and noded; rib C slightly less prominent and with or without nodes. Interspaces between ribs on later whorls with 3 to 8 threads; later whorls on some specimens (see Figure 20) only with R, A, B, and C, and their interspaces bearing only threads. Rib d just adapical to suture followed by very fine riblets. At suture, riblet with low elongate nodes; remainder of base with very fine, somewhat wavy riblets. Growth lines sigmoidal, maximum of antisinus somewhat posterior of midpoint of whorl. Suture impressed. Aperture round.

Holotype: CAS 61938.01.

Holotype dimensions: 27.5 mm height, 7 mm greatest diameter, specimen incomplete.

Type locality: CAS 61938.

Geologic age: Turonian, and probably early Coniacian.

Distribution: LOWER TURONIAN: Redding Formation, Bellavista Sandstone Member and Frazier Siltstone Member, Shasta County, northern California; Budden Canyon Formation, Gas Point Member, lower part, Shasta County, northern California. UPPER TURONIAN: Ladd Formation, Baker Canyon Member, Holz-Baker transition, and lower part Holz Shale Member, Santa Ana Mountains, Orange County, southern California. TURONIAN UNDIFFERENTIATED: Hornbrook Formation, Jackson County, southern Oregon. PROBABLY LOWER CONIACIAN: Hornbrook Formation, probably the Ditch Creek Siltstone Member, Siskiyou County, northern California.

Discussion: This study of Merriam's species is based on 239 specimens. Many of these are from the Hornbrook Formation, where the preservation is generally very good. A considerable number of specimens, however, are from the Redding Formation, east of Redding. Preservation of the Redding material is also generally very good.

Saul (1982:fig. 2 on p. 72) plotted the stratigraphic occurrence of this species in the Ladd Formation.

Merriam (1941) reported *Turritella tolenasensis* Merriam (1941:62, pl. 1, figs. 14, 15) from Cenomanian or Turonian strata in northern California. Saul (1983a:103), however, reported that Merriam's species is probably conspecific with *Turritella hearni* and that Merriam's type material of *T. tolenasensis* is definitely of Turonian and not Cenomanian age. In this present report, we put *T. tolenasensis* into synonymy with *T. hearni.*

Merriam (1941) reported *Turritella tolenasensis* subsp. Merriam (1941:62–63, pl. 1, fig. 12) from Tuscan Springs, Tehama County, northern California. Saul (1983a:102–104), however, tentatively put this subspecies into synonymy with *Turritella packardi* Merriam, 1941, an early to possibly middle Campanian gastropod.

Turritella iota Popenoe, 1937
(Figures 22–23)

Turritella iota Popenoe, 1937:401, pl. 49, fig. 8; Saul, 1982: 72 (chart).

Diagnosis: Adult whorls slightly concave to flattish with C rib strongest, forming narrow and projecting, weakly noded carina; posterior to carina sculpture consisting of three to four, weak spiral ribs alternating with weaker ones.

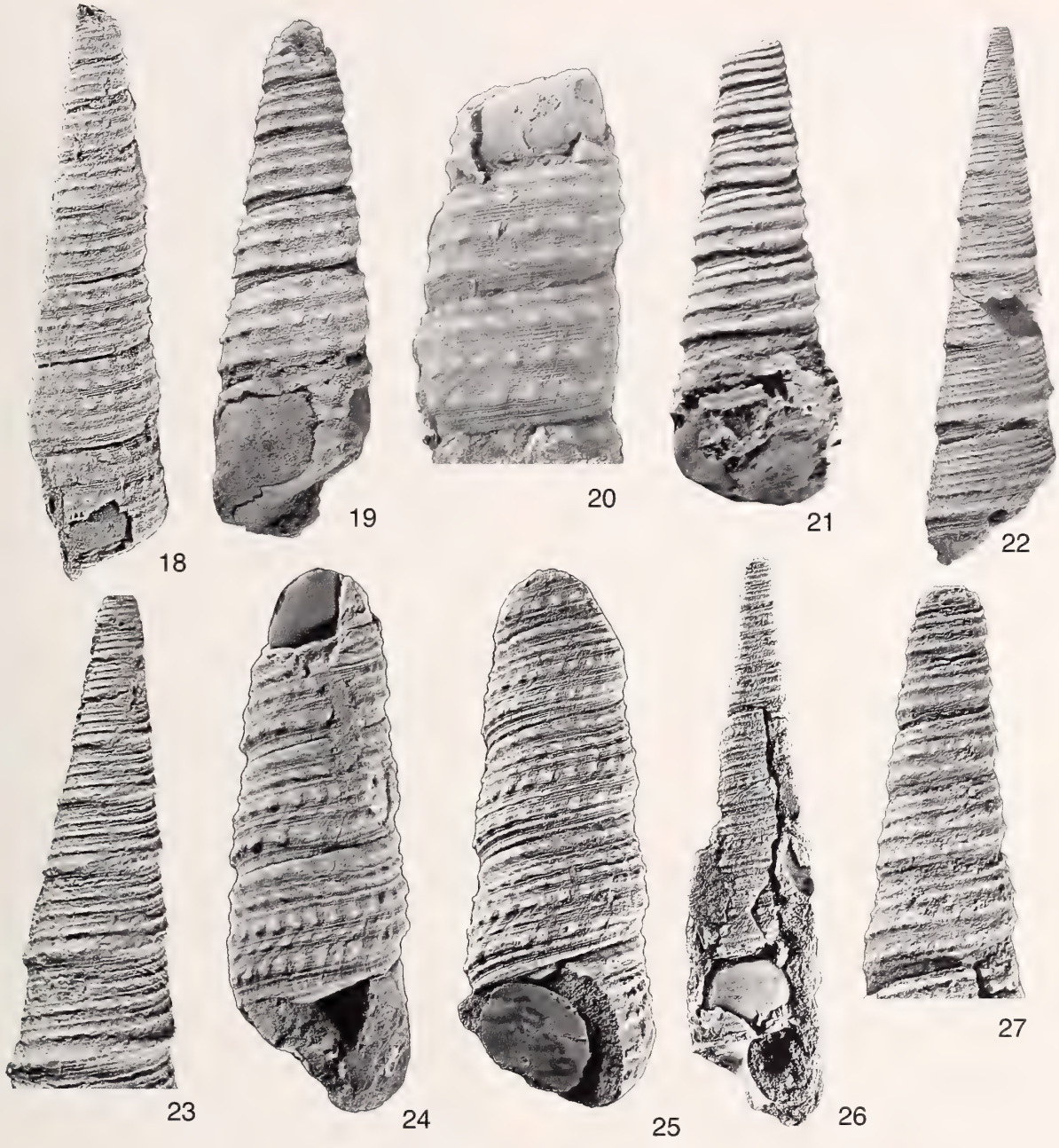
Description: Medium shell, slender. Pleural angle approximately 16°. Protoconch and earliest juvenile whorls unknown. Teleoconch whorls very shallowly concave to flattish. Suture impressed. Juvenile and early adult whorls (2 to 4.5 mm in diameter) with R, A, s, B, T, and C, with d appearing at approximately 2 mm diameter; R, A, B, and d weak and thin, C forming narrow and projecting carina. Adult whorls (greater than 5 mm diameter) similar to earlier whorls but with nodes on R, A, B, and C. Interspaces with threads, especially immediately posterior to carina. Carina of adult individuals rounded on slightly convex base. Base with noded rib adjacent to and paralleling d, another riblet toward mid base, and otherwise with fine striations. Basal ribs weakening toward aperture. Growth line sigmoidal, antisinus at midpoint of whorl and deepest at s.

Holotype: LACMIP 4186.

Holotype dimensions: 35.5 mm height, 9.6 mm greatest diameter, specimen incomplete.

Type locality: LACMIP 8178.

Geologic age: Late Turonian.



Explanation of Figures 18 to 27

Specimens coated with ammonium chloride. Figures 18–21. *Turritella hearni* Merrriam, 1941. Figure 18. Holotype CAS 61938.01, CAS loc. 61938, right-lateral view, ×3. Figure 19. Hypotype LACMIP 13317, LACMIP loc. 24251, abapertural view, ×4. Figure 20. Hypotype LACMIP 13318, LACMIP loc. 24251, right-lateral view, ×4.9. Figure 21. Hypotype CAS 69099.03, CAS loc. 69099, apertural view, ×7.4. Figures 22–23. *Turritella iota* Popenoe, 1937, LACMIP holotype 40673, LACMIP loc. 8178, left-lateral view. Figure 22. ×2.2. Figure 23. Tip of specimen shown in Figure 22, ×4.4. Figures 24–27. *Turritella* ***encina*** Squires & Saul, sp. nov. Figure 24. Holotype LACMIP 13319, LACMIP loc. 10798, apertural view, ×2.9. Figure 25. Paratype LACMIP 13320, LACMIP loc. 10900, apertural view, ×2.9. Figures 26–27. Paratype LACMIP 13321, LACMIP loc. 24336, apertural view. Figure 26. ×1.9. Figure 27. Tip of specimen shown in Figure 26, apertural view, ×5.6.

Distribution: LATE TURONIAN: Tuna Canyon Formation, lower part, west of Rustic Canyon, east-central Santa Monica Mountains, Los Angeles County, southern California; Ladd Formation, transition zone between Baker Canyon and Holz Shale members, and also lower Holz Shale, Santa Ana Mountains, Orange County, southern California.

Discussion: This study of Popenoe's species is based on 13 specimens. Most of them are from the lower part of the Tuna Canyon Formation at LACMIP loc. 26967 and show moderately good preservation.

This species is uncommon. It differs primarily from *T. petersoni* in having whorls that are concave, less numerous ribs, and a moderate carina at C. In addition, *T. iota* has weaker ribs of more uniform strength on the base.

Turritella iota differs from *T. hearni* in having stronger riblets on the base, crossed by strong growth lines that create a pitted surface. Popenoe (1937) indicated that it resembles somewhat a so-called "*Turritella whiteavesi* Anderson & Hanna," but Anderson (1958:152) noted that he and Hanna had never named a *T. whiteavesi.*

Saul (1982:fig. 2 on p. 72) reported on the occurrence of this species in the Ladd Formation, and she also reported that at its type locality, it is found with *Turritella hearni.*

Turritella ***encina*** Squires & Saul, sp. nov. (Figures 24–27)

Diagnosis: Adult whorls weakly convex, with four nearly equal-strength spiral ribs (B and C strongest), noded, and alternating with weaker ribs.

Description: Shell medium, slender. Pleural angle approximately 14°. Whorls weakly convex. Suture impressed. Protoconch and earliest juvenile unknown. Juvenile whorls (approximately less than 4.5 mm diameter) with three, nearly equal-strength equal spiral ribs (A, B, and C), all with weak nodes. Adult whorls (approximately greater than 5 mm in diameter) with four ribs (R, A, B, and C), each strongly noded and alternating with weaker, usually unnoded ribs, resulting in sculpture pattern of R, r_2, A, s, B, t, C, u, and d (d very weak). Ribs B and C strongest. Rib t with several threads posteriorly and anteriorly. Interspace between C and u with threads. Growth line sigmoidal, maxiumum of antisinus coincident with position of rib B. Aperture round.

Dimensions of holotype: 28.1 mm height, 9.7 greatest diameter 9.7 mm, specimen incomplete.

Holotype: LACMIP 13319.

Type locality: LACMIP loc. 10798, 122°04′45″W longitude, 40°38′N latitude.

Paratypes: LACMIP 13320 and 13321.

Geologic age: Santonian.

Distribution: SANTONIAN: Redding Formation, Member V, Old Cow and upper Clover creeks, Shasta County, northern California.

Discussion: This new species is based on 134 specimens, and most show good presevation.

Turritella ***encina*** is most similar to *Turritella hearni,* but *T.* ***encina*** differs by having ribs (s, t, and u) present, all of which are noded. *Turritella hearni* usually has only threads in its interspaces. In addition, on *T.* ***encina***, ribs B and C are approximately the same strength, rather than having rib B approximately the same strength as rib A.

Etymology: The new species is named for its occurrence in Oak Run, east of Redding; Spanish, ***encina*** meaning "oak."

Acknowledgments. We are grateful for access to the collections at CAS, LACMIP, and UCMP and for the loans provided by these institutions. Richard Soto (California State University, Northridge) kindly donated specimens of *Turritella seriatimgranulata.* The manuscript benefited from reviews by Steffen Kiel (Smithsonian Institution, National Museum of Natural History) and Edward Petuch (Florida-Atlantic University).

LITERATURE CITED

Akers, R. E. & T. J. Akers. 1997. Texas Cretaceous Gastropods. Texas Paleontology Series Publications 6. Houston Gem and Mineral Society: 340 pp.

Alderson, J. M. 1988. New age assignments for the lower part of the Cretaceous Tuna Canyon Formaton, Santa Monica Mountains, California. Geological Society of America Cordilleran Section Meeting, Las Vegas, Abstracts with Programs 20(3):139.

Allison, E. C. 1955. Middle Cretaceous Gastropoda from Punta China, Baja California, Mexico. Journal of Paleontology 29(3):400–432, pls. 40–44.

Allison, E. C. 1974. The type Alisitos Formation (Cretaceous, Aptian-Albian) of Baja California and its bivalve fauna. Pp. 21–59 in G. Gastil & J. Lillegrave (eds.), Geology of Peninsular California. Pacific Section, AAPG, SEPM, and SEG, Book 37. Los Angeles, California.

Allmon, W. D. 1988. Ecology of Recent turritelline gastropods (Prosobranchia, Turritellidae): current knowledge and paleontological implications. Palaios 3:259–284.

Allmon, W. D., D. S. Jones & N. Vaughan. 1992. Observations on the biology of *Turritella gonostoma* Valenciennes (Prosobranchia: Turritellidae) from the Gulf of California. The Veliger 35(1):52–63.

Almazan-Vazquez, E. 1990. Fauna Aptiano-Albiana del Cerro las Conchas, Sonora centro-oriental. Actas de la Facultad de Ciencias de la Tierra, Universidad Autonoma de Nuevo Leon 4:153–173, pls. 1–5.

Almgren, A. A. 1973. Upper Cretaceous foraminifera in southern California. Pp. 31–44 in A. E. Fritsche (ed.), Cretaceous Stratigraphy of the Santa Monica Mountains and Simi Hills, Southern California. Pacific Section, SEPM, Guidebook: Los Angeles, California.

Anderson, F. M. 1958. Upper Cretaceous of the Pacific coast. Geological Society of America Memoir 71:1–378, pls. 1–75.

Bandel, K. 1976. Observations on spawn, embryonic develop-

ment and ecology of some Carribbean lower Mesogastropoda. The Veliger 18(3):249–271.

Bandel, K., F. Riedel & H. Weikert. 1997. Planktonic gastropod larvae from the Red Sea: a synopsis. Ophelia 47(3): 151–202.

Böse, E. 1910. Monografia geológica y paleontológica del Cerro de Muleros cerca de Cuidad, Juarez, Estado de Chihuahua. Instituto Geologico de México Boletin 25, 193 pp., 48 pls.

Cobban, W. A. & J. B. Reeside, Jr. 1952. Correlation of the Cretaceous formations of the western interior of the United States. Bulletin of the Geological Society of America 63: 1011–1044.

Colburn, I. P. 1973. Stratigraphic relations of the southern California Cretaceous strata. Pp. 45–73 in A. E. Fritsche (ed.), Cretaceous Stratigraphy of the Santa Monica Mountains and Simi Hills, Southern California. Pacific Section, SEPM, Guidebook: Los Angeles, California.

Cox, L. R. 1959. Thoughts on the classification of the Gastropoda. Proceedings of the Malacological Society of London 33:239–261.

Davies, A. M. 1971. Tertiary Faunas, Vol. 1. The Composition of Tertiary Faunas. 2nd ed. Revised by F. E. Eames. George Allen & Unwin: London. 571 pp.

D'Orbigny, A. 1842–1843. Paléontologie Française. Description des Mollusques et Rayonnés Fossiles de France. Terrain Crétacés. Tome 2. Gastéropodes. Arthus-Bertrand: Paris. 456 pp. (1842), pls. 149–236 [in Atlas (1843)].

Frakes, L. A. 1999. Estimating the global thermal state from Cretaceous sea surface and continental temperature data. Pp. 49–57 in E. Barrera & C. C. Johnson (eds.), Evolution of the Cretaceous Ocean-Climate System. Geological Survey of America Special Paper 332.

Gabb, W. M. 1864. Description of the Cretaceous fossils. California Geological Survey, Palaeontology 1:57–243, pls. 9–32.

Gabb, W. M. 1869. Cretaceous and Tertiary fossils. California Geological Survey, Palaeontology 2:1–299, pls. 1–36.

Givens, C. R. 1974. Eocene molluscan biostratigraphy of the Pine Mountain area, Ventura County, California. University of California Publications in Geological Sciences 109, 107 pp., 11 pls.

Gradstein, F. M., J. G. Ogg & A G. Smith. 2004. A Geologic Time Scale. Cambridge University Press: Cambridge, England. 589 pp.

Grant, U. S., IV & H. R. Gale. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California. Memoirs of the San Diego Society of Natural History. Volume 1. 1036 pp., 32 pls.

Haller, B. 1882. Zur Kenntniss der Muriciden. Eine vergleichend-anatomische Studie, 1, Theil, Anatomie des Nervensystemes. Denkschriften der kaiserlichen Akademie der Wissenschaften, Wien. Mathematisch-Naturwissenschaftliche Klasse 45:87–106.

Haq, B. U., J. Hardenbol & P. R. Vail. 1987. Chronology of fluctuating sea levels since the Triassic. Science 235:1156–1167.

Johnson, C. C. 1999. Evolution of Cretaceous surface current circulation patterns, Caribbean and Gulf of Mexico. Pp. 329–343 in E. Barrera & C. C. Johnson (eds.), Evolution of the Cretaceous Ocean-Climate System. Geological Society of America Special Paper 232.

Kaim, A. 2004. The evolution of conch ontogeny in Mesozoic open sea gastropods. Palaeontologia Polonica 62:1–183, figs. 1–140.

Kilmer, F. H. 1984. Geology of Cedros Island, Baja California, Mexico. Privately Published: Arcata, California. 69 pp.

Lamarck, J. B. de. 1799. Prodrome d'une nouvelle classification des coquilles. Mémories de la Société d'histoire Naturelle de Paris. Pp. 63–91.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Editio decima, reformata, Vol. 1. Regnum Animale. Laurentii Salvii: Stockholm. 824 pp.

Loel, W. & W. H. Corey. 1932. The Vaqueros Formation, lower Miocene of California. 1. Paleontology. University of California Publications Bulletin of the Department of Geological Sciences 22:31–410, pls. 4–65.

Lovén, S. L. 1847. Malacozoologii. Öfversigt af Kongliga Ventenskaps-Akademinens Förhandlingar, pp. 175–199, pls. 2–6.

Marwick, J. 1957a. New Zealand genera of Turritellidae, and the species of *Stiracolpus*. New Zealand Geological Survey Paleontological Bulletin 27, 55 pp., 5 pls.

Marwick, J. 1957b. Generic revision of the Turritellidae. Proceedings of the Malacological Society 32(4):144–166.

Matsumoto, T. 1960. Upper Cretaceous ammonites of California. Part 3. Memoirs of the Faculty of Science, Kyushu University, Series D, Geology, Special Volume 2, 204 pp., 2 pls.

Merriam, C. W. 1941. Fossil turritellas from the Pacific coast region of North America. University of California Publications, Bulletin of the Department of Geological Sciences 26(1):1–214, pls. 1–41.

Murphy, M. A. & P. U. Rodda. 1960. Mollusca of the Cretaceous Bald Hills Formation of California. Journal of Paleontology 34(5):835–858, pls. 101–107.

Murphy, M. A., P. U. Rodda & D. M. Morton. 1969. Geology of the Ono Quadrangle, Shasta and Tehama counties, California. California Division of Mines and Geology Bulletin 192, 28 pp.

Petuch, E. J. 1976. An unusual molluscan assemblage from Venezuela. The Veliger 18:322–325, figs. 1–8.

Popenoe, W. P. 1937. Upper Cretaceous Mollusca from southern California. Journal of Paleontology 11(5):379–402, pls. 45–49.

Popenoe, W. P. 1973. Southern California Cretaceous formations and faunas with especial reference to the Simi Hills and Santa Monica Mountains. Pp. 15–29, pls. 1–3, in A. E. Fritsche (ed.), Cretaceous Stratigraphy of the Santa Monica Mountains and Simi Hills, Southern California. Pacific Section, SEPM, Guidebook: Los Angeles, California.

Richter, G. & G. Thorson. 1975. Pelagische Prosobranchier-Larven des Golfes von Neapel. Ophelia 13:109–163,

Rodda, P. U. 1959. Geology and paleontology of a portion of Shasta County, California. Unpub. Ph.D. Dissertation. University of California, Los Angeles. 204 pp., 14 pls.

Roemer, F. 1849. Texas, mit Besonderer Rücksicht auf Deutsche Auswanderung und die Physischen Verhältnisse des Landes nach Eigener Beobachtung Geschildert. Bonn. 469 pp.

Roemer, F. 1852. Die Kreidebildungen von Texas und ihre Organischen Einschlüsse. 100 pp., 11 pls.

Saul, L. R. 1978. The North Pacific Cretaceous trigoniid genus *Yaadia*. University of California Publications in Geological Sciences 119:1–65, pls. 1–12.

Saul, L. R. 1982. Water depth indications from Late Cretaceous mollusks, Santa Ana Mountains, California. Pp. 69–76 in D. J. Bottjer, I. P. Colburn & J. D. Cooper (eds.), Late Cretaceous Depositional Environments and Paleogeography, Santa Ana Mountains, Southern California. Pacific Section, SEPM, Field Trip Volume and Guidebook: Los Angeles, California.

SAUL, L. R. 1983a. *Turritella* zonation across the Cretaceous-Tertiary boundary, California. University of California Publications in Geological Sciences 125:1–163, pls. 1–6.

SAUL, L. R. 1983b. Notes on Paleogene turritellas, venericardias, and molluscan stages of the Simi Valley area, California. Pp. 71–80 in R. L. Squires & M. V. Filewicz (eds.), Cenozoic Geology of the Simi Valley Area, Southern California. Pacific Section, SEPM, Volume and Guidebook: Los Angeles, California.

SAUL, L. R. 1986. Pacific west coast Cretaceous molluscan faunas: time and aspect of changes. Pp. 131–136 in P. L. Abbott (ed.), Cretaceous Stratigraphy Western North America. Pacific Section, SEPM, Volume 46: Los Angeles, California.

SAUL, L. R. & R. L. SQUIRES. 1998. New Cretaceous Gastropoda from California. Palaeontology 41(3):461–488, pls. 1–3.

SCHRÖDER, M. 1995. Frühontogenetische Schalen jurassischer und untercretazischer Gastropoden aus Norddeutschland und Polen. Palaeontographica, Abt B, 238(1):1–95.

SHRIMER, H. W. & R. R. SHROCK. 1944. Index Fossils of North America. Massachusetts Institute of Technology. Eighth printing. The M. I. T. Press: Cambridge, Massachusetts. 837 pp.

SLITER, W. V., D. L. JONES & C. K. THROCKMORTON. 1984. Age and correlation of the Cretaceous Hornbrook Formation, California and Oregon. Pp. 89–98 in T. H. Nilsen (ed.), Geology of the Upper Cretaceous Hornbrook Formation, Oregon and California. Pacific Section, SEPM, Vol. 42: Los Angeles, California.

SOHL, N. F. 1987. Cretaceous gastropods: contrasts between Tethys and the temperate provinces. Journal of Paleontology 61:1085–1111.

SQUIRES, R. L. 1984. Megapaleontology of the Eocene Llajas Formation, Simi Valley, California. Natural History Museum of Los Angeles County, Contributions in Science 350, 76 pp., figs. 1–19.

SQUIRES, R. L. 1987. Eocene molluscan paleontology of the Whitaker Peak area, Los Angeles and Ventura counties, California. Natural History Museum of Los Angeles County, Contributions in Science 388, 93 pp., 135 figs.

SQUIRES, R. L. & L. R. SAUL. 2003a. Additions to Late Cretaceous shallow-marine gastropods from California. The Veliger 46(2):145–161, figs. 1–43.

SQUIRES, R. L. & L. R. SAUL. 2003b. New Cretaceous cerithiform gastropods from the Pacific slope of North America. Journal of Paleontology 77(3):442–453, figs. 1–25.

SQUIRES, R. L. & L. R. SAUL. 2004a. Cretaceous corbulid bivalves of the Pacific slope of North America. The Veliger 47(2):103–129, figs. 1–62.

SQUIRES, R. L. & L. R. SAUL. 2004b. The pseudomelaniid gastropod *Paosia* from the marine Cretaceous of the Pacific slope of North America and a review of the age and paleobiogeography of the genus. Journal of Paleontology 78(3): 4184–500, figs. 1–5.

STAINBROOK, M. A. 1940. Gastropoda of the Kiamichi shale of the Texas Panhandle. Texas University Bulletin 3945:705–716, pl. 33.

STANTON, T. W. 1947. Studies of some Comanche pelecypods and gastropods. U.S. Geological Survey Professional Paper 211, 256 pp., 67 pls.

STEWART, R. B. 1927. Gabb's California fossil type gastropods. Proceedings of the Academy of Natural Sciences of Philadelphia 78(for 1926):287–447, pls. 20–32.

THORSON, G. 1957. Bottom communities (sublittoral or shallow shelf). Pp. 461–534 in J. W. Hedgeth (ed.), Treatise on Marine Ecology and Paleoecology. Geological Society of America Memoir 67, Vol. 1, Ecology.

WEAVER, C. E. 1943. Paleontology of the marine Tertiary formations of Oregon and Washington. University of Washington Publications in Geology 5(3 parts):1–789, pls. 1–104.

WHITE, C. A. 1879. Contributions to invertebrate paleontology, no. 1, Cretaceous fossils of the western states and territories. U. S. Geological and Geographical Survey of the Territories Annual Report 11:273–319.

YONGE, C. M. & T. E. THOMPSON. 1976. Living Marine Molluscs. William Collins Sons & Co.: Glasgow, Scotland. 288 pp.

APPENDIX

LOCALITIES

CAS 1291. On old Peterson Ranch, 6.4 km NE of Sites, Lodoga Quadrangle (15 minute, 1943), west side of Sacramento Valley, Colusa County, northern California. Great Valley Group, informal Antelope Shale, just below the Venado Formation. Age: Cenomanian. Collector: Unknown.

CAS 2335. Outcrop just beneath rim rock of Logan Ridge, approximately 1.6 km NE of old Peterson Ranch House, 4.8 km NE of Sites, Lodoga Quadrangle (15 minute, 1943), west side of Sacramento Valley, Colusa County, northern California.

CAS 61938. Approximately 6.4 km N of Montague and approximately, 304 m NE of old Hagerdorn Ranch House, Yreka Quadrangle (30 minute, 1939), Siskiyou County, northern California. Hornbrook Formation, probably Ditch Creek Member. Age: Probably early Coniacian. Collector: Unknown.

CAS 69098. [= LACMIP 23903]. Large gray limestone nodules in gray mudstone on S bank of creek, 582 m and 73 m N of SW corner of section 29, T. 30 N, R. 6 W, Ono Quadrangle (15 minute, 1952), Shasta County, northern California. Budden Canyon Formation, Gas Point Member, lower part. Age: Turonian. Collectors: P. U. Rodda, August, 1955.

CAS 69099. [= LACMIP 23817]. Sandstone bed in mudstone section, third major W-heading tributary of North Fork Cottonwood Creek, S of mouth of Huling Creek, 762 m E and 549 m S of SE corner of section 29, T. 30 N, R. 6 W, Ono Quadrangle (15 minute, 1952), Shasta County, northern California. Budden Canyon Formation, Gas

Point Member, lower part. Age: Early Turonian. Collector: P. U. Rodda, August, 1956.

CAS 69104. [= LACMIP 23893]. Texas Springs, Redding Quadrangle (15 minute, 1946) Shasta County, northern California. Budden Canyon Formation, Chickabally Member. Age: Late early Albian. Collector: Unknown.

CAS 69106. [= LACMIP 23808]. Shale bank, left side of Roaring River, about 1.2 km above the dam at the basal conglomerates, 914 m N and 1066 m E of SW corner of section 1, T. 29 N, R. 7 W, Ono Quadrangle (15 minute, 1952), Shasta County, northern California. Budden Canyon Formation, Gas Point Member. Age: Early Turonian. Collectors: W. P. Popenoe and W. Findlay, 1933; P. U. Rodda, 1956.

CAS 69107. [= LACMIP 23937]. On side of small creek, SE 1/4 of section 20, T. 30 N, R. 6 W, Ono Quadrangle (15 minute, 1952), Shasta County, northern California. Budden Canyon Formation, Gas Point Member, lower part. Age: Early Turonian. Collector: P. U. Rodda, August, 1956.

CAS 69111. North Fork of Cottonwood Creek, Ono Quadrangle (15 minute, 1943), Shasta County, northern California. Budden Canyon Formation, Bald Hills Member. Age: Cenomanian. Collector: P. U. Rodda.

LACMIP 8178. [= CIT 984]. On W side of Rose Canyon, 205 m S and 329 m W of NE corner of section 2, T. 6 S, R. 7 W, Santiago Peak Quadrangle (7.5 minute, 1954), Santa Ana Mountains, Orange County, southern California. Ladd Formation, middle part of Holz-Baker transition zone. Age: Late Turonian. Collector: W. P. Popenoe, October 15, 1933.

LACMIP 10798. Massive sandstones interbedded with conglomerates on S side of high E-W trending ridge, S side of Oak Run Valley, 998 m S54°50′W from SE corner of section 10, T. 32 N, R. 2 W, Millville Quadrangle (15 minute, 1953), Shasta County, northern California. Redding Formation, Member V. Age: Early Santonian. Collectors: W. P. Popenoe and C. Ahlroth, July 1, 1936.

LACMIP 10900. South side of Old Cow Creek, NE ¼, SW ¼ of section 20, T. 32 N, R. 1 W, Millville Quadrangle (15 minute, 1953), Shasta County, northern California. Redding Formation, Member V. Age: Santonian. Collector: V. C. Church, April 12, 1937.

LACMIP 15741. Float material from about the middle of the island in a downfaulted synclinal block, Cedros Island, Baja California, Mexico. Valle Group (member unknown). Age: Cenomanian or Turonian. Collector: F. H. Kilmer.

LACMIP 23470. On E side of North Fork of Cottonwood Creek, section 16, T. 30 N, R. 6 W, Ono Quadrangle (15 minute, 1953), Shasta County, northern California. Budden Canyon Formation, Bald Hills Member. Age: Cenomanian? Collector: P. U. Rodda, September, 1955.

LACMIP 24251. Sandstone cropping out along ridge by ranch road, 914 m W and 259 m S of NE corner of section 26, T. 46 N, R. 6 W, 14.5 km NE of Yreka, Yreka Quadrangle (30 minute, 1939), Siskiyou County, northern California. Hornbrook Formation, Osburger Gulch Sandstone Member. Age: Turonian. Collectors: M. A. Murphy, W. P. Popenoe, and T. Susuki, August 30, 1951.

LACMIP 24336. Fossiliferous float concretion in siltstone on N side of Clover Creek Valley, 365 m N and 244 m E of SW corner of section 13, T. 32 N, R. 2 W, Millville Quadrangle (15 minute, 1953), Shasta County, northern California. Redding Formation, Member V. Age: Early Santonian. Collector: W. P. Popenoe, August 15, 1954.

LACMIP 25272. South side of Cherry Hill about 100m W of first big turn on Cherry Hills Road and approximately 1 km N of Pioneer Road, west boundary of NW ¼ of section 12, R. 1 W, T. 38 S, Medford Quadrangle (15 minute, 1938), near Phoenix, Jackson County, southwestern Oregon. Hornbrook Formation. Age: Turonian. Collector: Takeo Susuki, 1962.

LACMIP 26967. Small exposure of coarse-grained, poorly sorted sandstone at bottom of NW-flowing tributary to main fork of Garapito Creek, 450 m S and 2835 m E of NW corner of section 5, T. 1 S, R. 16 W, Topanga Quadrangle (7.5

minute, 1952, photorevised, 1981), Santa Monica Mountains, Los Angeles County, southern California. Tuna Canyon Formation, lower part. Age: Late Turonian. Collector: J. M. Alderson, December 31, 1981.

LACMIP 27242. East bank of Cottonwood Creek about 0.4 km downstream from mouth of Huling Creek, fossiliferous concretions weathering out from near top of conglomerate of Bald Hills Member and just below beginning of slabby sandstones and mudstones of Gas Point Member, approximately 533 m N and 274 m E of SW corner of section 16, T. 32 N, R. 6 W, Ono Quadrangle (15 minute, 1953), Shasta County, northern California. Budden Canyon Formation, Bald Hills Member. Age: Cenomanian. Collector: W. P. Popenoe, April, 1954.

UCMP A-9521. Punta China, 25 km SE of Ensenada, northern Baja California, Mexico. Alisitos Formation. Age: Late Aptian. Collector: Probably E. C. Allison, 1960s.

Instructions to Authors

The Veliger publishes original papers on any aspect of malacology. All authors bear full responsibility for the accuracy and originality of their papers.

Presentation

Papers should include an abstract (approximately 5% of the length of the manuscript), Introduction, Materials and Methods, Results, and Discussion. Short notes should include a one-sentence abstract. In taxonomic papers, all names of taxa must be accompanied by author and date of publication, and by a full citation in the bibliography. In papers on other subjects and in the non-taxonomic portions of taxonomic papers, author and date of names need not be accompanied by a full citation. All references to new molecular sequences must be lin ked to GenBank.

Literature Cited

Each citation should consist of a complete list of authors, with initials, date of publication, full title of article of chapter, names of all editors of books, publisher and place of publication for all books, journal titles spelled out in full, volume number (and, where appropriate, issue number), and inclusive pagination. Authors must be consistent about punctuation. Every reference in the text must be accompanied by a citation in the bibliography, and all entries in the bibliography must be mentioned in the body of the paper. Authors should cross-check the bibliography with the text.

Submitting manuscripts

All manuscripts must be submitted as Word files, double spaced, plus one double-spaced paper copy. If you are submitting images on disc, please include a directory of the files and a hard copy printout of each figure. Halftones should be at least 300 ppi; graphics in TIFF or EPS format.

Send manuscripts, proofs, books for review, and correspondence on editorial matters to:

Geerat J. Vermeij
Editor, *The Veliger*
Department of Geology
University of California at Davis
One Shields Avenue
Davis, CA 95616

veliger@geology.ucdavis.edu
T 530.752.2234
F 530.752.0951

In the cover letter, authors should briefly state the point of the paper, and provide full and electronic addresses of at least three reviewers who have not previously seen the manuscript. If authors feel strongly that certain reviewers would be inappropriate, they should indicate reasons for their views.